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ENVIRONMENTAL REGULATION OF GROWTH IN BLACK BRANT

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

August 2002

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Abstract

Body size is an important determinant of life history traits such as survival and fecundity. There is a positive correlation between growth during the first summer and final body size in goose populations. I examined how environmental factors influence growth in Black Brant (*Branta bernicla;* hereafter brant) goslings. Growth declined seasonally and varied among brood-rearing areas. However, the pattern was not consistent among years. Models containing only environmental and maternal effects explained 75% of variation in gosling mass, indicating that little of the observed variation in size is directly of genetic origin. Heritability did not differ from zero for both mother-daughter and father-daughter regressions.

I also conducted an experiment to study the effect of gosling density on food abundance, feeding behavior, and development of brant goslings, in two habitat types important to brant: (1) *Carex subspathacea* grazing lawns and (2) slough levees which contain *Triglochin palustris.* Variation in grazing pressure was experimentally manipulated. Biomass and offtake of *C. subspathacea* was higher in lightly grazed plots than in heavily grazed plots even though goslings within heavily grazed plots spent more time feeding. Within slough levee habitat there were no differences between heavily and lightly grazed plots in either biomass or offtake of *T. palustris.* Peck rates were lower in slough levee habitat than in grazing lawns.

Change in mass over an eight hour trial was positively correlated with the amount of forage biomass in the plot at the start of the trial. I found no variation in internal morphometrics or body composition among goslings.

I also examined the relationship between total forage available within a brood-rearing area, the number of birds using the area, and gosling growth. Annual variation in use of brood-rearing areas was correlated with forage availability. Gosling mass was negatively correlated with brood numbers when examined across all areas, however, within each brood-rearing area, the relationship between mass and numbers of birds was positive. I did not see a relationship between estimates of food availability (per m^2) and brood numbers. Spatial variation in growth among habitats may result from habitats varying in quality and quantity of forage.

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Acknowledgments

While the thesis may have only one author, and the submitted chapters, only two or three, the work presented in this book would not have been possible without the effort of many other people.

First, my committee members have been a tremendous help in the formation of this final product, and each deserve individual recognition. Dave McGuire brought forth a modeling perspective, which helped me develop and analyze the numerous factors that go into growth models. With all theses, there are difficult times. I especially appreciate the individual sacrifices Dave made to help me with my thesis.

Roger Ruess has been a great asset both in the field and in the lab. Roger's great knowledge of the Yukon-Kuskokwim Delta ecosystem and ability to think deeply about a question helped me to formulate some of my ideas.

Eric Rexstad became a friend and a colleague. Beyond his mastery of statistics and quantitative ecology, Eric's dedication to teaching and advising should be used as benchmarks for any aspiring professor. The demands he places on excellence and hard work, are exceeded only by his dedication to the process.

Jim Sedinger has also become as much a great friend as he is a great advisor. His insight into my research has been invaluable. I cannot count the number of hours Jim has spent just sitting and discussing research; surpassed only by the number of hours we spent talking about hockey. Special thanks must be given also to the entire Sedinger

family – Jim, Connie, Ben, and Katie, who have opened their house for numerous Thanksgivings, and Easters. They were most certainly my family away from home.

The help and support I received from friends and fellow grad students can not go unrecognized. Almost everyone associated with the research on the Y-K Delta has helped me. Brian Person, Mike Eichholz, Jason Schamber, and Bill O'Connell have been great researchers and great friends. So many great ideas have come from just being in the lab with them.

Mark Lindberg, Joel Schmutz, Maggie MacCluskie, and Paul Flint have also all helped me throughout with insightful and stimulating conversation. Being a part of the Sedinger Waterfowl Lab has been exciting. I have never experienced anything as intellectually challenging and interesting as discussing ecology with these great folks.

I don't think any acknowledgements would be complete without recognizing the important role my parents have played in my development, not only for the past six years but the past 33 years. Their unwavering love and support has allowed me to pursue this career. Without their initial stimulus, I may never have developed such an intense interest in nature and ecology.

And what would a brother be without a sister. Sandy is a great person who is always happy. I thank her and James for their love and friendship always.

Chapter 1. General Introduction

The period of growth and development is among the most important periods in the life cycle of organisms, and in particular for arctic nesting geese such as black brant (Sedinger 1992, Stearns 1992). Not only is mortality extremely high during the growth period, thereby influencing the population dynamics of geese, but variation in growth has been linked to a number of important life-history traits such as survival and fecundity (Davies et al. 1988, Alisauskas and Ankney 1990, Francis et al. 1992, Sedinger et al. 1995, Choudhury et al. 1996, van der Jeugd and Larsson 1998).

Arctic summers have short growing seasons, and young must grow and rapidly fledge. For larger species, this requires young to fledge at a much smaller fraction of final adult mass, usually at the cost of other development, such as reproductive maturation (Sedinger 1992). Consequently, larger species must continue their physiological development during the winter, and forego breeding their first year.

While small taxa may benefit from the significant demographic advantages of breeding within their first year, there are also advantages to being larger such as the ability to defend their nest against predators, improved thermoregulation, improved fasting endurance, and improved digestive efficiency due to large gut capacity, which enables them to use a more plentiful, yet less nutritious food base.

Within a species, and in particular for geese, larger individuals are generally more successful. Along with the advantages just described, larger birds within a species also have been shown to have increased first-year survival, be more successful in

competing for mates, have increased access to food in winter, and produce larger clutches (Davies et al. 1988, Alisauskas and Ankney 1990, Francis et al. 1992, Sedinger et al. 1995, Choudhury et al. 1996, van der Jeugd and Larsson 1998).

While final adult body size is positively correlated with size at the end of the first summer, and larger adult body size has substantial life-history benefits, selection for high growth rates may occur for other reasons as well. Predation before fledging is probably the largest source of mortality for young during this period (Zicus 1981, Eberhardt et al. 1989b, Flint et al. 1995, Schmutz et al. 2001). Therefore, there is a significant fitness advantage to an individual that can reduce the amount of time before fledging (Bosque and Bosque 1995).

Because selection is for relatively high growth rates, there is the potential for increased influence of nutrition on growth rates, fledging size, and body composition. Arctic geese are obligate herbivores during the breeding season (Owen 1980). In many areas, the growing season is less than 100 days. To grow rapidly and fledge within this short period, goslings must maximize nutrient intake. Because vegetation has relatively poor nutritional quality compared to other food resources used by waterfowl (Sedinger et al. 1992), geese must not only feed at high rates, but be highly selective of their forage intake (Sedinger and Raveling 1984, Sedinger and Raveling 1990).

The overall objective of my research was to examine how variation in quality and availability of forage can influence gosling growth. In this thesis, I present the results in three parts.

In the first part (Chapter 2), I examined those factors that influence growth. Over the 12 years of the project and the 4 years I was in the field, we collected considerable data on many of the factors associated with gosling growth. However, natural selection cannot act on environmental variation. The amount of genetic variation present in a phenotypic trait determines the response to selection on that trait. Therefore, I also examined the amount of phenotypic variation in growth associated with the parents, as well as the heritability of mass, culmen and tarsus measures.

Second, many studies have observed variation in body size, or changes in behavior, and attributed it to variation in forage availability. However, few experiments have been designed to address this issue. Therefore, in Chapters 2 and 3, I present results from a captive experiment designed to directly assess the impact variation in grazing pressure can have on food availability, and consequently how this variation in available food translates into variation in growth and development of goslings.

Finally, spatial variation in growth can be attributed to a number of factors, such as the density of birds or total food base available. Therefore it is important to present results that address variation in availability of food on a spatial scale. This study addresses how the number of birds within an area interacts with available food, and consequently gosling mass.

Together the results from these three objectives, divided into four chapters, contribute to the understanding of how growth of geese is influenced by the environment. In conjunction with previous results, that have shown that body size greatly influences

life history traits in geese, the results of my thesis demonstrate the importance of quality habitat to the future fitness of individual brant geese.

LITERATURE CITED

Alisauskas, R.T., and C.D. Ankney. 1990. Body size and fecundity in lesser snow geese. Auk 107:440-443.

Bosque, C., and M.T. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. American Naturalist 145:234-260.

Choudhury, S., J.M. Black, and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. Ibis 138:700-709.

Davies, J.C., R.F. Rockwell, and F. Cooke. 1988. Body-size variation and fitness components in lesser snow geese (*Chen caerulescens caerulescens*). Auk 105:639-648.

Eberhardt, L.E., R.G. Anthony, and W.H. Rickard. 1989. Survival of juvenile Canada Geese during the rearing period. Journal of Wildlife Management 53:372-377.

Flint, P.L., J.S. Sedinger, and K.H. Pollock . 1995. Survival of juvenile black brant during brood rearing. Journal of Wildlife Management 59:455-463.

Francis, C.M., M.H. Richards, F. Cooke, and R.F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology 73:1346-1362.

Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd, London.

Schmutz, J.A., B.J. Manly, and C.P. Dau. 2001. Effects of gull predation and weather on survival of Emperor Goose goslings. Journal of Wildlife Management 65:248-257.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger, J.S., and D.G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger, J.S., and D.G. Raveling. 1990. Parental behavior of cackling Canada geese during brood rearing: Division of labor within pairs. Condor 92:174-181.

Sedinger, J.S. 1992. Ecology of prefledging waterfowl. Pages 109-127 *in* Ecology and management of breeding waterfowl (Batt, D.J.B., A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, Editors). University of Minnesota Press, Minneapolis, MN.

Sedinger, J.S., R.G. White, and W.E. Hauer. 1992. Heat increment of feeding and partitioning of dietary energy in yearling Black Brant. Canadian Journal of Zoology 70:1047-1051.

Stearns, S. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

van der Jeugd, H.P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese Branta leucopsis in relation to fledgling characteristics. Journal of Animal Ecology 67:953-966.

Zicus, M.C. 1981. Canada goose brood behavior and survival estimates at Crex Meadows, Wisconsin. Wilson Bulletin 93:207-217.

Chapter 2. Variation in Growth of Black Brant is of Environmental Origin

ABSTRACT

Body size is an important determinant of life history traits such as survival and fecundity in many terrestrial vertebrates. In addition, there is a positive correlation between growth during the first summer and final body size in some populations. Thus, understanding factors that influence gosling growth is essential for understanding fitness in geese. We examined the importance of environmental factors, such as annual, seasonal and spatial variation in habitat quality, that influence growth in Black Brant (*Branta bernicla nigricans)* goslings. We also examined maternal effects of egg size, maternal age and maternal identity. Growth was lower for goslings that hatched later during the summer season. Male goslings were affected by the seasonal decline to a greater extent than female goslings. Additionally, we found that in the most populated brood-rearing areas, the growth rate of Black Brant goslings declined during the late 1980s, probably associated with increasing density. In contrast growth rate of goslings generally increased during the 1990s and was associated with habitat modification by the geese themselves. Growth rate varied significantly among brood-rearing areas used by brant, although the pattern was not consistent among years. Older females (4 years of age or greater) produced larger goslings than did younger females. After controlling for

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Chapter 2 formatted for submittal to Ecology.

female age, gosling mass at about 4½ weeks of age was positively correlated with egg size. Overall, models containing only environmental and maternal effects explained 75% of variation in gosling mass, indicating that little of the observed variation in size in this population is directly of genetic origin.

We examined heritability of adult size using a sample of individuals that were initially webtagged as goslings and subsequently weighed as adults. Heritability did not differ from zero for both mother-daughter and father-daughter regressions. The combination of low heritabilities and large explanatory power of environmental or maternal variables suggests that variation in size in the Black Brant population is primarily of environmental or maternal origin. Our results suggest that selection on body size has been stronger in Black Brant than in other geese, thereby reducing the genetic variation in growth. These findings further suggest that improving our understanding of mechanisms used to translate environmental factors into growth is essential to understanding adaptation by Black Brant to their subarctic environment.

INTRODUCTION

The influence of body size on fitness components such as fecundity and survival has been demonstrated in several species (Davies et al. 1988, Clutton-Brock et al. 1988, Alisauskas and Ankney 1990, Cooch et al. 1992, Sedinger et al. 1995, Choudhury et al. 1996, van der Jeugd and Larsson 1998). Understanding the mechanism by which body size affects fitness, however, is difficult. Indirectly, body size can determine social status and affect acquisition of a mate or territory quality (Aldrich and Raveling 1983, Richner et al. 1989, Shine 1989, Owen and Black 1989, Nilsson 1990). Individuals with larger

adult body size can produce better quality offspring (Viallefont et al. 1995) and more offspring (Alatalo and Lundberg 1986, Cooch et al. 1991a, Sedinger et al. 1995, Barbraud et al. 1999). Larger birds also survive at a higher rate and reproduce longer (Owen and Black 1989, Francis et al. 1992, Schmutz 1993, Sedinger et al. 1995, van der Jeugd and Larsson 1998). Over-winter survival is also positively correlated with body-size (Leihikoinen 1986, Schmutz and Ely 1999).

While selection acts on final body size, growth rate of young is also subject to trade-offs to optimize fitness (Ricklefs 1968, Lack 1968). With growing seasons less than 100 days, goslings must grow rapidly and fledge before fall freeze-up. Before fledging, young birds are more susceptible to predation and weather and have significantly lower survival than juveniles that are older (Zicus 1981, Eberhardt et al. 1989a, Flint et al. 1995, Schmutz et al. 2001). Selection may act on growth rates to minimize the time young birds experience higher mortality rates (Bosque and Bosque 1995; but see, Ricklefs et al. 1998).

Arctic geese are obligate herbivores during the breeding season (Owen 1980). Growing goslings forage on a nutrient-limited and poorly digestible diet (Sedinger et al. 1992). Owing to small gut capacity and need for fast growth rates, goslings feed most of the daylight hours (Sedinger and Raveling 1990) and are highly selective of their diet (Sedinger and Raveling 1984). Variation in quality and availability of this forage, both spatially and temporally, can directly translate into variation in growth of goslings

(Sedinger and Flint 1991, Cooch et al. 1991a, Cooch et al. 1993, Aubin et al. 1993, Sedinger et al. 1998, Leafloor et al. 1998, Sedinger et al. 2001).

The amount of genetic variation present in a phenotypic trait determines the response to selection on that trait (Stearns 1992). Phenotypic variation is the sum of environmental and genetic variation plus twice the environmental X genetic covariation (Stearns 1992). Heritability should be low for life history traits because selection has reduced genetic variation (Gustafsson 1986, Stearns 1992). Nevertheless, many goose life history traits have considerable broad-sense heritability (Findlay and Cooke 1983, Larsson and Forslund 1991, Sedinger et al. 1997), although it has been difficult to control for environmental and maternal effects in these estimates (Larsson et al. 1998)

Parental quality, although sometimes difficult to separate from environmental effects, can influence growth in avian species (Coulson and Thomas 1985, Verhulst and Tinbergen 1991, Hipfner 1997, Nisbet et al. 1998). The results are less conclusive for species with precocial young, such as waterfowl (Lepage and Desrochers 1999), but variation in a parent's ability to protect its young, or create access to high quality forage should influence growth and survival of young (Larsson and Forslund 1992).

In this paper, we examine the effects of variation in environment and parental quality, on growth and body size of goslings in an arctic nesting species of goose, Black Brant (*Branta bernicla nigricans*; hereafter "brant") within a single colony in western Alaska. We also present heritability estimates of these traits within brant.

METHODS

Study area. –All data analyzed for this paper were collected from the Yukon-Kuskokwim (Y-K) Delta, on the west coast of Alaska at the Tutakoke River Black Brant Colony (61°N, 165°W), and associated brood-rearing areas, between 1987–1998. See Sedinger et al. (1998) and Fig. 1 for descriptions of study area. This coastal area is characterized by low growing saltmarsh vegetation dominated by graminoids and *Carex* spp. (Kincheloe and Stehn 1991). The nesting colony is located in the "Camp" and Kash-Tut areas of Fig. 1. Brood-rearing areas, we studied, are located within the nesting colony and upstream along both the Tutakoke and Kashunuk Rivers. The most-distant brood-rearing area we sampled in this study was the Onumtuk/Emperor Bend brood-rearing area and is located 30km up the Kashunuk River.

Methods. - Each year we searched up to 49, 50-meter radius plots every 4 days throughout the egg laying period. In these areas, every nest was found during the egg-laying stage. For the remainder of the colony, we intensively searched areas for nests associated with banded females. These nests were found throughout laying, incubation and hatch. At each nest, all eggs were labeled for identification and their length and width measured (± 0.1 mm). Egg volume was calculated from linear egg measurements using the same equation as previous studies (Sedinger and Flint 1991). If a specific egg did not have length and width measurements (e.g., gosling already hatched), then mean length and width for other eggs from the same nest were used, as variation in egg size

within clutches was much smaller than variation among clutches (Flint and Sedinger 1992).

At hatch, we visited each nest associated with a marked parent and attached individually coded fish fingerling tags to the webbing of each gosling (Alliston 1975, Sedinger and Flint 1991). If possible, goslings were webtagged during the pipping stage of hatch so we could assign them to an individual egg. We assigned webtags only to goslings still in the nest bowl that were less than 2 days old. We placed 17,222 webtags on goslings during the study (Table 1). We calculated relative hatch date by subtracting the date of peak of hatch for all goslings in a year, from an individual gosling's actual hatch date.

During brood-rearing, approximately 4.5 weeks after peak of hatch (range of gosling ages: 19-39 days), we captured geese during large banding drives. During this period, adults were flightless and goslings had not fledged. Each banding drive was organized such that it represented a specific brood-rearing area. While not all brood-rearing areas were sampled every year, only one brood-rearing area was sampled for less than 9 years.

During capture and banding, we examined each gosling for a webtag. We measured culmen, diagonal tarsus length (± 0.1mm each), and mass (± 5 g) of each webtagged gosling (Dzubin and Cooch 1992). We determined sex for each gosling by cloacal examination (Owen 1980).

We classified known aged mothers of goslings into young (less than 4 years of age) and old (4 years or older). Previous analysis has shown that more than 70% of all females breed by their third year, and additionally if females have not bred by 5 years of age, they have a very low probability of ever breeding (Sedinger et al. 2001). Thus, mothers that are 4 years or older have most likely bred at least once. Thus, females less than four years old had nested less than twice, while those older than four had likely nested more than two times.

To analyze the effects of environmental and parental variables on gosling mass at banding, we used the maximum likelihood method in the PROC MIXED procedure of SAS (SAS Institute 1999). Model selection was based on Akaike's Information Criterion corrected for sample size (AIC_c). AIC_c decreased as the log-likelihood declined, but increased as parameters were added to the models. Thus, AIC_c balances model fit with model complexity. Parameter estimates were averaged across models within two AIC_c units of the model with the lowest AIC_c (Burnham and Anderson 1998).

The adult female associated with the nest was assumed to be the genetic mother of the eggs found within the nest. The female was considered a random variable and goslings were nested within individual females. Because many of the factors influencing gosling growth also affect the entire brood, the female was used as the sampling unit to prevent pseudo-replication (Hurlbert 1984, Loonen et al. 1997). All results reported are the result of model averaged least squares means and calculated standard errors from the final models (Anderson et al. 2000).

We examined the contribution of females to gosling growth in 2 different ways. First, while considering female a random variable, the covariance test option in PROC MIXED partitioned random effect variation into the designated random effects and residual variance (SAS Institute 1999). Also, PROC NESTED was used to examine variation associated with female before additional analysis.

To estimate heritability, single parent-offspring regressions (son on father, daughter on father, son on mother, and daughter on mother) as well as midparent offspring regressions were performed using mean adult (after second year) mass, tarsus, and culmen measurements for both goslings and parents (Falconer 1981). Because brant are sexually dimorphic, measurements were standardized by the following standard normal transformation:

$$\frac{(x_{ob} - \bar{x}_{sex})}{\sigma_{sex}}$$

where x_{ob} = observed data, $\bar{x}_{sex}$ = mean for that sex, σ_{sex} =sex specific standard deviation (Lynch and Walsh 1998). If an individual was captured more than once as an adult, the average measurement from all captures was used. Only goslings from the first recaptured brood for an adult were included in the regression. Heritability and standard error estimates were calculated by doubling the slope and standard error estimates from the parent-offspring regressions (Falconer 1981).

RESULTS

Because of variation in the number of nesting geese, nest success, and field effort, the number of webtagged goslings recaptured varied annually between 63 and 461 (Table 1). We recaptured 3,133 of 17,222 webtagged goslings over 13 years of study (Table 1). During the entire study gosling age at capture ranged from 19 to 39 days old ($\bar{x}$ = 30.8). Gosling mass varied from 200 grams to 1180 grams and mass varied by more than 500 grams for goslings of the same age. A regression of mass on age yielded a significant linear trend of 27 grams per day. These results were comparable to results from captive goslings (Herzog 2002). Our final model, however, included a brood-rearing area*year interaction (Table 2). Because each banding drive occurred on a unique brood-rearing area, and each drive was less than 1 day in length, there was no variation in capture date within each brood-rearing area*year combination. Age was highly correlated with both capture date and hatch date. Relative hatch date was calculated by adjusting hatch date for the peak of hatch that year. Thus, age became confounded with relative hatch date in any model that included a brood-rearing area*year interaction. To examine how variation in age and relative hatch date was explained by brood-rearing area and year we performed ANOVA's with brood-rearing area and year as main effects on both age and relative hatch date. A model with year and brood-rearing area alone explained 73% of the variation in gosling ages observed. However, only 14% of the variation in relative hatch date was explained with the same model. Thus, when a model included brood-rearing area, year, and the brood-rearing area*year interaction, we chose to include

relative hatch date in the model and removed the age variable. In fact, age was non-significant during model selection in the analysis of variation in mass.

Goslings hatching later were smaller than earlier hatching goslings (Table 2). In addition, the most likely model included a sex by hatch-date interaction. The sex by hatch date interaction suggested that male goslings were more severely affected by hatch date than were females, losing 11% more in mass than females for each day later in the season that they hatched. After controlling for all other factors, for each day later a gosling hatched, the model predicted a male gosling was 37.4 grams smaller, and a female 33.4 grams smaller than goslings hatched a day earlier. However, these estimates were not significantly different from each other (P=0.0849). Both squared and cubic forms of relative hatch date were included in initial models but were not selected in likely models and the variables were subsequently removed.

Egg volumes ranged from 56 cm^3 to 108 cm^3. Larger goslings came from eggs with larger volume (slope = 3.2 ± 0.5 grams/cm^3). Thus, goslings could vary in mass by 140-190 grams from variation in egg size alone. While there was less than 1% difference in egg volume between males and females at hatch, at capture male goslings were considerably larger than female goslings. After controlling for all other factors, male goslings weighed 708 ± 6 grams, whereas female goslings weighed 670 ± 6 grams. Male and female goslings weighed 54% and 59% of their adult counterparts, respectively, during banding.

Environmental Variation.- There was considerable annual variation in gosling mass at banding (Fig. 2). In addition, for all selected models, we observed an interaction between brood-rearing area and year. Within a given year, goslings from the brood-rearing area where the largest goslings were found were over 30% greater in mass than goslings from the brood-rearing area with the smallest goslings. Similarly, within a brood-rearing area, annual variation in mass exceeded 30%. The final model suggested variation in patterns of annual variation in gosling mass dynamics among brood-rearing areas. Detailed analysis using the slice option in PROC MIXED showed that each brood-rearing area varied among years. However in several years (1987, 1988, and 1997), gosling size did not substantially differ among brood-rearing areas (Fig. 2). Models for tarsus and culmen were similar except there was no interaction between brood-rearing area and year (Table 2; Fig. 3).

Role of parental quality and individual female.- In the final model, age-class (<4 or ≥ 4 years old) of the mother positively influenced gosling mass at banding after controlling for other variables. At banding, goslings from older mothers were nearly 24 grams larger than goslings from younger mothers. Models that included the age of the fathers of goslings captured at banding were not selected ($\Delta AIC_c >> 5$). Estimates of an effect of a father's age were less than half of that observed with mother's age (goslings from older fathers were 8 ± 5 grams larger than goslings from younger fathers), and not significant (P=0.158).

Because female was used as a random effect in the primary model, we were able to compare the restricted maximum likelihood estimates of the variance components among females and residual error to examine the proportion of residual variation attributable to females. Variation among females represented 37% of the total residual variation ($Z=7.54$, $P<0.0001$) remaining after controlling for the other factors in the final model and only 15% of all variation when run in a model without controlling for any other factors. Whether included in the model with mother, or run separately, individual fathers did not explain any of the residual variation in the models ($Z=0.01$, $P>0.5$). We found significant variation in female age among brood-rearing areas. However, older females were found in the brood-rearing areas that produced the smallest goslings. Nearly all of the broad-sense heritability estimates for mass, tarsus, and culmen did not differ from zero except for those estimated using father-son regressions (Table 3). All father-son regressions were significant but based on only 3 data points.

DISCUSSION

Our findings indicate that after controlling for egg size and the sex of the gosling, variation in growth of brant is predominantly of environmental and maternal origin. Similar to many studies that examined the effect of size of eggs or hatching mass on gosling growth (Ankney 1980, Thomas and Peach Brown 1988, Cooch et al. 1991a), we found a significant positive relationship between egg size and gosling mass at banding. While the relationship between egg size and gosling mass is highly significant, the influence on gosling mass is much smaller than other factors in our model. Across the

range of egg sizes, there is less than a 12% difference in mass at banding between goslings hatching from eggs differing by 30% in volume. Ankney (1980) showed that the correlation between egg size and body size declined as Lesser Snow Goose goslings got older. Our analysis shows that in brant, an egg size-body size relationship still exists near fledging but the relationship explains very little of total variation in gosling size. Additionally, selection against smaller individuals may reduce the range of adult mass further reducing variation found in adult brant and weakening any correlations between mass and other variables.

Gosling growth and final size typically decline with later hatching date (Larsson and Forslund 1991, Sedinger and Flint 1991, Cooch et al. 1991a) and our results show a similar negative effect of hatch date on gosling mass at banding. Males were disproportionately affected by hatching later, although a model that did not include the hatch-date x sex interaction was nearly as likely ($\Delta AIC_c = 0.7$) Cooch et al. (1997) also found that male goslings were more sensitive than female goslings to factors influencing growth rates. Cooch et al. (1997) hypothesized that male goslings, which have increased energy demands due to higher growth rates, did not survive as well to fledging as female goslings in the broods of younger females. Our finding that growth of male goslings is more negatively affected by hatching later than female goslings is consistent with the Cooch et al. (1997) hypothesis that males are more sensitive than females to the quality and quantity of food.

Environmental variation.- Spatial and temporal variation in quality of habitat influences growth and final body size in most geese (Sedinger and Flint 1991, Larsson and Forslund 1991, Cooch et al. 1991a, Cooch et al. 1991a, Cooch et al. 1991b, Aubin et al. 1993, Loonen et al. 1997, Fowler and Ely 1997). Our models indicate that growth varied substantially among individual brood-rearing areas (Fig. 2). Standing crop nitrogen levels and carbon-nitrogen ratios (both indices of food quality) vary among brood-rearing areas at Tutakoke (Person et al. 1998). Indices of grazing intensity and number of broods within each brood-rearing area suggest that per capita food availability also varies among brood-rearing areas (Person et al. 1998, Herzog 2002). Areas of low forage biomass also have higher brood numbers and lower gosling mass (Herzog 2002, Person et al. In press).

The role of parental age in gosling growth.- We found that goslings of older females were significantly larger at banding than goslings from younger females. Variation in growth may be influenced by the ability of parents to provide access to higher quality foraging locations. Social status and experience of parents increases with age and is associated with improved reproductive performance (Lamprecht 1986, Owen and Black 1989, Rockwell et al. 1993, Black and Owen 1995).

Clutch size increases with age in geese (Finney and Cooke 1978, Forslund and Larsson 1992, Rockwell et al. 1993, Sedinger et al. 1998). We did not find a positive relationship between brood size and gosling growth as did Cooch et al. (1991a), potentially, because the positive relationship we observed between gosling growth and

female age obscured a relationship between brood-size and growth rate. In a manipulation experiment, Loonen et al. (1999) showed that goslings from larger broods of Barnacle Geese (*Branta leucopsis*) grew larger than goslings from smaller broods. In a similar study of manipulated clutches, however, we did not detect such a positive relationship (Herzog unpublished). It is possible that some of the effect of brood size on gosling growth in other studies is actually attributable to female age and experience, and our controlling for female age precluded us from detecting an association between growth and brood size. In models that included brood size there was a weak, but non-significant (P=0.097) positive slope between brood size and gosling size.

Spatial variation in growth and the lack of ideal free distribution.- Most research on spatial variation in gosling growth has examined variation in growth among goslings from different colonies (but see Larsson and Forslund 1991). Sedinger et al. (2001) showed significant variation in size among brant from 3 different Alaskan colonies. However, even for the Tutakoke Colony, we found that brant goslings captured in brood-rearing areas only 5-10 km apart differ by more than 25 % (160 grams) in mean body mass.

Within a few days after hatch, brant move from nests to brood-rearing areas as far as 30 km away (Flint 1993, Lindberg and Sedinger 1998). Once on a brood-rearing area, however, movement is generally restricted to a 1-2 square km home range (Flint pers. comm.). Significant variation in gosling mass among brood-rearing areas indicates that the distribution of brant among brood-rearing areas is not ideal free with respect to

growth rates of goslings. Because growth is an important determinant of future fitness (Lindström 1999, Lummaa and Clutton-Brock 2002) variation in growth rate among brood-rearing areas is synonymous with variation in mean fitness among brood-rearing areas. It is, thus, important to understand patterns of use of brood-rearing areas.

We envision three hypotheses that could explain lack of an ideal free distribution of brant broods with respect to growth.

1. Adults do not have complete information about the distribution of abundance and quality of plant foods. It seems unlikely that adults with broods could assess food quality and abundance on all brood-rearing areas during a summer. Given imperfect knowledge, the risk of moving to a brood-rearing area of poorer quality than one presently occupied may be great enough to limit exploration and movement. A more conservative response for brant would be to change brood-rearing areas between years based on their experience in the first year. Lindberg et al. (1995) and Lindberg and Sedinger (1998) found fidelity to brood-rearing areas, while moderately high, was less than fidelity to nesting area, suggesting that a substantial number of adult brant change brood-rearing areas between years.

An additional complication for adult brant is that relative quality of brood-rearing areas is not constant across years. Grazing lawns upon which goslings depend heavily are temporally (Person unpublished) and spatially dynamic (Person et al. 1998). Furthermore, shifting use of brood-rearing areas changes brood density and per capita food abundance from one year to the next. We intend to examine whether or not

decisions to change brood-rearing areas are related to growth rate of goslings as a test of this hypothesis.

2. Costs of using particular brood-rearing areas or movement between brood-rearing areas may counterbalance the advantages of otherwise high quality areas that support rapid growth. If predation rates vary sufficiently among brood-rearing areas, recruitment of goslings from areas varying substantially in growth rate could be comparable. Glaucous Gulls (*Larus hyperboreous*) are important predators of goslings on the Y-K Delta (Schmutz and Hobson 1998). We intend to assess relative survival rates of goslings on different brood-rearing areas in the future.

3. Brant families may arrange themselves so that families of generally higher social status are together on higher quality brood-rearing areas, while families of low social status are relegated to poor quality areas. Hughes et al. (1994) found that broods that hatched earlier used higher quality habitat than broods that hatched later. Our results however, are not entirely consistent with this hypothesis, as factors associated with female quality, such as hatch date do not differ among brood-rearing areas (P=0.439). We did detect a variation in parental age among brood-rearing areas, but while we found older parents produced larger goslings within brood-rearing areaa, brood-rearing areas that produced the smallest goslings had older parents than other areas.

Broad-sense heritability estimates and the role of body size selection.- With few samples, especially for father-son, and mother-son regressions, our ability to detect statistically significant heritabilities was low. It is interesting that the single-parent

regression with the smallest samples (father-son) is also the one where our estimate of heritability was significant. However, we believe this to be a statistical artifact. The fact that the values were extremely high, two of which were well outside the possible range for heritabilities, suggests that these results are not biologically meaningful. We performed a power analysis to examine our ability to detect heritabilities at our given sample sizes (Lynch and Walsh 1998). At $\alpha = 0.05$, and power at 90%, our mother-daughter offspring regressions (N=62) allow us only to be confident about detecting $h^2 > 0.60$ (Fig. 4). While midparent regressions are more powerful, our sample size (N=31) is much lower for families where both parents have been captured and measured and allows us to only be confident about detecting $h^2 > 0.69$. Nonetheless, Larsson and Forslund (Larsson and Forslund 1992) estimated heritabilities of body size traits in Barnacle Geese large enough that we would have detected them, except when goslings experienced poor growing conditions (Larsson 1993).

We found that females contribute less than 15% of the overall variation in gosling mass at banding and we could account for 75% of the variation in gosling size using models accounting only for environmental or maternal effects. Our data also indicate there is considerable variation in mass of goslings from the same mother (among years). Variation in size of goslings from individual females did not result from females changing mates, because brant retain the same mates for life (Owen et al. 1988, Black and Owen 1989). Effects of female age and annual variation in availability of forage (e.g. switching brood-rearing areas) all contribute to inter-annual variation. Thus, gosling

growth is under substantial environmental influence. Our observations that heritability estimates, from both parent-offspring and midparent-offspring regressions, are not different from zero and the small amount of variation in gosling growth attributable to individual females indicates that very little of the variation in growth and final body size was of genetic origin within the brant population at Tutakoke. The relatively minor importance of additive genetic variation differs from other goose species (Davies et al. 1988, Larsson and Forslund 1992, Cooke et al. 1995) and suggests that body size has been under much stronger selective pressures in brant than in other geese (Larsson et al. 1998). We suggest that brant are near minimum size for an avian herbivore in the arctic.

In the context of other recent studies (Cooch et al. 1991a, Larsson and Forslund 1991, Forslund and Larsson 1992, Sedinger et al. 1995, Cooch et al. 1997, Leafloor et al. 1998, Sedinger et al. 1998), our findings demonstrate the importance of environmental factors as well as maternal effects, such as parental age, and egg size in determining growth in brant goslings on the Y-K Delta. These findings further suggest that improving our understanding of mechanisms used to translate environmental factors into growth is essential to understanding adaptation by organisms to their environment.

ACKNOWLEDGEMENTS

This study was funded by grants from the National Science Foundation (OPP 92 14970), Angus Gavin, and the Center for Global Change at the University of Alaska Fairbanks. Logistic support was provided from United States Fish & Wildlife Service, Yukon Delta National Wildlife Refuge. In addition, many people assisted in over 13

summers of fieldwork including N.D. Chelgren, M.W. Eichholz, P.L. Flint, D.S. Johnson, M.J. Knoche, M.S. Lindberg, W.T. O'Connell, B.T. Person, J.L. Schamber, P.A. Svete, and J.B. Wenzel. This manuscript benefited from comments by A.D. McGuire, E.A. Rexstad, and R.W. Ruess.

LITERATURE CITED

Alatalo, R.V., and A. Lundberg. 1986. Heritability and selection on tarsus length in the Pied Flycatcher (*Ficedula hypoleuca*). Evolution 40:574-583.

Aldrich, T.W., and D.G. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada geese. Auk 100:670-679.

Alisauskas, R.T., and C.D. Ankney. 1990. Body size and fecundity in lesser snow geese. Auk 107:440-443.

Alliston, W.G. 1975. Web-tagging ducklings in pipped eggs. Journal of Wildlife Management 45:625-628.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.

Ankney C.D. 1980. Egg weight, survival, and growth of lesser snow goose goslings. Journal of Wildlife Management 44:174-182.

Aubin, A.E., A. Dzubin, E.H. Dunn, and C.D. MacInnes. 1993. Effects of summer feeding area on gosling growth in Snow Geese. Ornis Scandinavica 24:255-260.

Barbraud, C., H. Weimerskirch, G.G. Robertson, and P. Jouventin. 1999. Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). Journal of Animal Ecology 68:1179-1192.

Black, J.M., and M. Owen. 1995. Reproductive performance and assortative pairing in relation to age in Barnacle Geese. Journal of Animal Ecology 64:234-244.

Bosque, C., and M.T. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. American Naturalist 145:234-260.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference : A practical information-theoretic approach. Springer, New York.

Choudhury, S., J.M. Black, and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. Ibis 138:700-709.

Cooch, E.G., R.L. Jefferies, R.F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: An example in the lesser snow goose. Oecologia 93:128-138.

Cooch, E.G., D. Lank, R. Robertson, and F. Cooke. 1997. Effects of parental age and environmental change on offspring sex ratio in a precocial bird. Journal of Animal Ecology 66:189-202.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: Evidence of environmental degradation?. Journal of Animal Ecology 60:483-496.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1992. Is there a positive relationship between body size and fecundity in lesser snow geese?. Auk 109:667-673.

Cooke, F., R.F. Rockwell, and D.B. Lank. 1995. The Snow Geese of La Pérouse Bay: Natural selection in the wild. Oxford University Press, New York.

Coulson, J.C., and C. Thomas. 1985. Differences in the breeding performance of individual kittiwake gulls, *Rissa tridactyla* (L.). Pages 489-503 *in* Behavioral Ecology: Ecological consequences of adaptive behavior (Sibly, R.M. and R.H. Smith, Eds.). Blackwell Press, London.

Davies, J.C., R.F. Rockwell, and F. Cooke. 1988. Body-size variation and fitness components in lesser snow geese (*Chen caerulescens caerulescens*). Auk 105:639-648.

Dzubin, A., and E.G. Cooch. 1992. Measurements of geese. General field methods. California Waterfowl Thesis, Sacramento

Eberhardt, L.E., R.G. Anthony, and W.H. Rickard. 1989. Movement and habitat use by Great Basin Canada goose broods. Journal of Wildlife Management 53:740-748.

Falconer, D.S. 1981. Introduction to quantitative genetics, 2nd edition. Longman Inc., New York.

Findlay, C.S., and F. Cooke. 1983. Genetic and environmental components of clutch size variance in a wild population of Lesser Snow Geese (*Anser caerulescens caerulescens*). Evolution 37:724-734.

Finney, G., and F. Cooke. 1978. Reproductive habits in the snow goose: the influence of female age. Condor 80:147-158.

Flint, P.L., and J.S. Sedinger. 1992. Reproductive implications of egg-size variation in the black brant. Auk 109:896-903.

Flint, P.L., J.S. Sedinger, and K.H. Pollock. 1995. Survival of juvenile black brant during brood rearing. Journal of Wildlife Management 59:455-463.

Forslund, P., and K. Larsson. 1992. Age-related reproductive success in the barnacle goose. Journal of Animal Ecology 61:195-204.

Fowler, A.C., and C.R. Ely. 1997. Behavior of cackling Canada geese during brood rearing. Condor 99:406-412.

Francis, C.M., M.H. Richards, F. Cooke, and R.F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology 73:1346-1362.

Gustafsson, L. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. American Naturalist 128:761-764.

Herzog, M.P. 2002. Environmental regulation of growth in black brant. Ph.D. Dissertation. University of Alaska Fairbanks.

Hipfner, J.M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. Condor 99:353-360.

Hughes, R.J., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536-545.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Kincheloe, K.L., and R.A. Stehn. 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim Delta, Alaska. Canadian Journal of Botany 69:1616-1627.

Lack, D. 1968. Ecological adaptation for breeding in birds. Methuen, London.

Lamprecht, J. 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). Behaviour 96:28-48.

Larsson, K. 1993. Inheritance of body size in the barnacle goose under different environmental conditions. Journal of Evolutionary Biology 6:195-208.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619-636.

Larsson, K., and P. Forslund. 1992. Genetic and social inheritance of body and egg size in the barnacle goose (*Branta leucopsis*). Evolution 46:235-244.

Larsson, K., H.P. van der Jeugd, I.T. van der Veen, and P. Forslund. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. Evolution 52:1169-1184.

Leafloor, J.O., C.D. Ankney, and D.H. Rusch. 1998. Environmental effects on body size of Canada geese. Auk 115:26-33.

Leihikoinen, E. 1986. Dependence of winter surivival on size in the great tit *Parus major*. Ornis. Fenn. 63:10-16.

Lepage, D., and A.G.G. Desrochers. 1999. Seasonal decline of growth and fledging success in Snow Geese *Anser caerulescens*: an effect of date or parental quality? Journal of Avian Biology 30:72-78.

Lindberg, M.S., and J.S. Sedinger. 1998. Ecological significance of brood-site fidelity in black brant: Spatial, annual, and age-related variation. Auk 115:436-446.

Lindberg, M.S., J.S. Sedinger, and E.A. Rexstad. 1995. Estimating nest fidelity of adult female black brant with multi-state modeling and geographic information systems. Journal of Applied Statistics 22:725-735.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.

Loonen, M.J.J.E., K. Oosterbeek, and R.H. Drent. 1997. Variation in growth of young and adult size in Barnacle Geese *Branta leucopsis*: evidence for density dependence. Ardea 85:177-191.

Loonen M.J.J.E., L.W. Bruinzeel, J.M. Black, and R.H. Drent. 1999. The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. Journal of Animal Ecology 68:753-768.

Lynch, M. and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Inc., Sunderland, MA.

Nisbet, I.C.T., J.A. Spendelow, J.S. Hatfield, J.M. Zingo, and G.A. Gough. 1998. Variations in growth of Roseate Tern chicks: II. Early growth as an index of parental quality. Condor 100:305-315.

Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd, London.

Owen, M., and J.M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Person, B.T., C.A. Babcock, and R.W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific black brant geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243-259.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110:419-451.

Ricklefs, R.E., J.M. Starck, and M. Konarzewski. 1998. Internal constraints on growth in birds. Pages 266-287 *in* Avian Growth and Development: Evolution within the altricial-precocial spectrum (Starck, J.M. and R.E. Ricklefs, Eds.). Oxford University Press, New York.

Rockwell, R.F., E.G. Cooch, C.B. Thompson, and F. Cooke. 1993. Age and reproductive success in female lesser snow geese: Experience, senescence and the cost of philopatry. Journal of Animal Ecology 62:323-333.

SAS Institute. 1999. The SAS System for Windows. Version: 8.0.

Schmutz, J.A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. Condor 95:222-225.

Schmutz, J.A., and C.R. Ely. 1999. Survival of greater white-fronted geese: Effects of year, season, sex, and body condition. Journal of Wildlife Management 63:1239-1249.

Schmutz, J.A., and K.A. Hobson. 1998. Geographic, temporal, and age-specific variation in diets of Glaucous Gulls in western Alaska. Condor 100:119-130.

Schmutz, J.A., B.J. Manly, and C.P. Dau. 2001. Effects of gull predation and weather on survival of Emperor Goose goslings. Journal of Wildlife Management 65:248-257.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger, J.S., M.S. Lindberg, and N.D. Chelgren. In Press. Age-specific breeding probability in Black Brant: effects of population density. Journal of Animal Ecology

Sedinger, J.S., M.S. Lindberg, M. Eichholz, and N. Chelgren. 1997. Influence of hatch date versus maternal and genetic effects on growth of black brant goslings. Auk 114:129-132.

Sedinger, J.S., M.S. Lindberg, B.T. Person, M.W. Eichholz, M.P. Herzog, and P.L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J.S., and D.G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger, J.S., and D.G. Raveling. 1990. Parental behavior of cackling Canada geese during brood rearing: Division of labor within pairs. Condor 92:174-181.

Sedinger, J.S., M.P. Herzog, B.T. Person, M.T. Kirk, T. Obritschkewitsch, P.P. Martin, and B.A. Anderson. 2001. Large scale variation in growth of black brant goslings related to food availability. Auk 118:1088-1095.

Sedinger, J.S., R.G. White, and W.E. Hauer. 1992. Heat increment of feeding and partitioning of dietary energy in yearling Black Brant. Canadian Journal of Zoology 70:1047-1051.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64:419-464.

Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.

Thomas, V.G., and H.C. Peach Brown. 1988. Relationships among egg size, energy reserves, growth rate, and fasting resistance of Canada goose goslings from southern Ontario. Canadian Journal of Zoology 66:957-964.

van der Jeugd, H.P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67:953-966.

Verhulst, S., and J.M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major* . Journal of Animal Ecology 60:269-282.

Viallefont, A., F. Cooke, and J.D. Lebreton. 1995. Age-specific costs of first-time breeding lesser snow geese. Auk 112:67-76.

Zicus, M.C. 1981. Canada Goose Brood Behavior and Survival Estimates at Crex Meadows, Wisconsin. Wilson Bulletin 93:207-217.

Table 2.1. Summary of Sample Sizes for Brant webtagged at the Tutakoke River Black Brant Colony between 1987 - 1998

Year	Number of Nests Found	Number of Nests Used	Webtags Attached	Webtags Recaptured	Percent Recapture	Number of Unique Broods
1987	176	176	670	63	.0940	26
1988	384	232	903	135	.150	19
1989	349	242	1197	188	.157	75
1990	427	269	1235	231	.187	114
1991	396	244	1200	216	.180	99
1992	656	289	1568	235	.150	98
1993	502	292	1518	203	.134	89
1994	594	423	1919	193	.101	111
1995	927	549	2508	324	.129	161
1996	625	312	1769	461	.261	153
1997	430	260	1025	176	.172	79
1998	368	239	1710	254	.149	106
Total	5834	3514	17222	3133	.182	1139

Table 2.2. General linear mixed models describing variation in growth of Black Brant goslings at Tutakoke River Black Brant Colony. Female was included as a random effect in all models. All models with $\Delta AIC_c \leq 5$ are shown.

Response Variable	Explanatory Variables[a]	Number of Parameters	ΔAIC_c	AIC_c weight
Mass	YR, BA, Sex, FA, EV, AHD, YR* BA, Sex*AHD	63	0.0	0.537
	YR, BA, Sex, FA, EV, AHD, YR* BA	62	0.7	0.463
Culmen	YR, BA, Sex, EV, AHD	21	0.0	0.461
	YR, BA, Sex, FA, EV, AHD	22	0.4	0.378
	YR, BA, Sex, FA, EV, AHD, Sex*AHD	23	2.1	0.161
Tarsus	YR, BA, Sex, FA, EV, AHD	22	0.0	0.679
	YR, BA, Sex, FA, EV, AHD, Sex*AHD	23	2.0	0.250
	YR, BA, Sex, EV, AHD	21	4.5	0.072

[a] Abbreviations for explanatory variables: YR – year, BA – brood-rearing area, FA – female ageclass, EV – egg volume, AHD – adjusted hatch date.

Table 2.3. Heritability (h^2) estimates from mother-daughter, mother-son, father-daughter, father-son, and midparent-offspring regressions.

Regression	Sample Size	Heritability	SE	P
MASS				
Mother-Daughter	62	-0.178	0.422	0.676
Mother-Son	13	2.46	0.838	0.012
Father- Daughter	37	-0.140	0.302	0.645
Father-Son	3	-1.554	0.190	0.015
Offspring-Midparent	31	-0.196	0.528	0.713
TARSUS				
Mother-Daughter	62	0.468	0.276	0.096
Mother-Son	13	0.722	0.370	0.075
Father- Daughter	37	-0.018	0.386	0.964
Father-Son	3	0.350	0.026	0.005
Offspring-Midparent	31	0.470	0.524	0.377
CULMEN				
Mother-Daughter	62	0.346	0.458	0.452
Mother-Son	13	1.042	0.876	0.257
Father- Daughter	37	-0.340	0.330	0.311
Father-Son	3	1.488	0.268	0.031
Offspring-Midparent	31	0.420	0.642	0.518

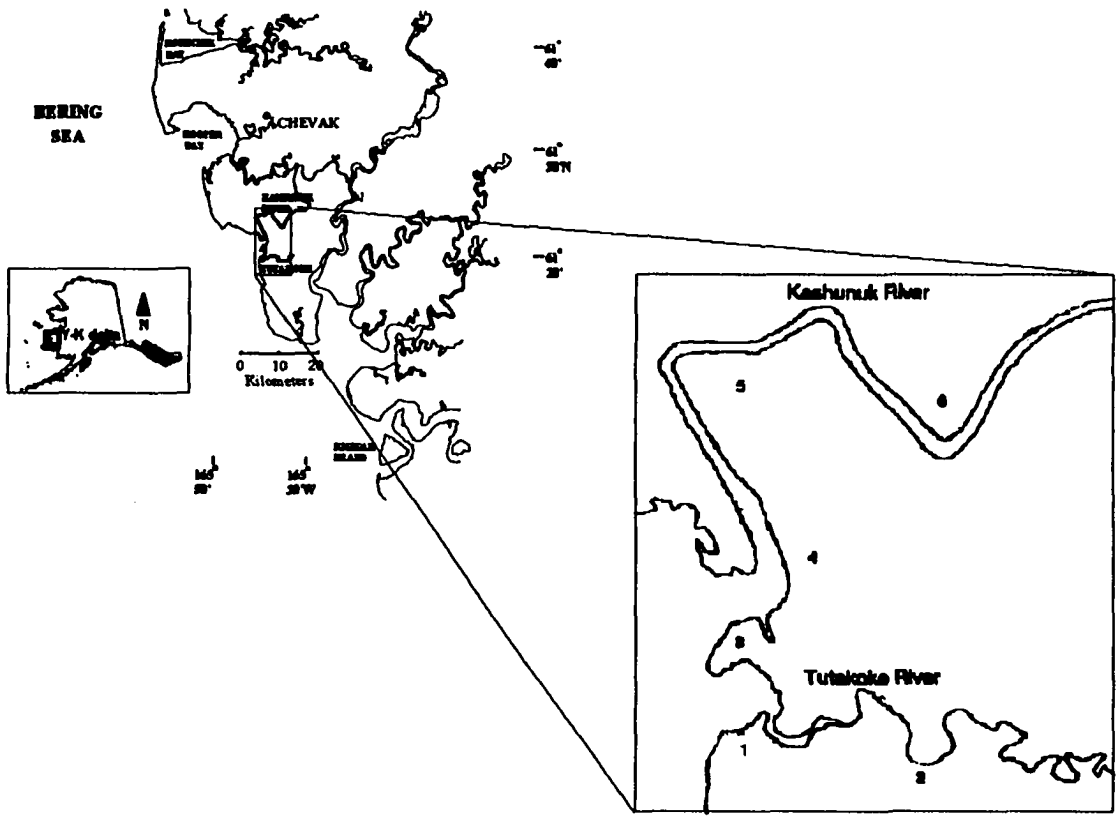

Figure 2.1. Brood-rearing areas at the Tutakoke Black Brant Colony. The number of years sampled is in parentheses. 1 = Tutakoke Camp (11 years), 2=Upper Tutakoke (12 years), 3 = Kash-Tut (8 years), 4=Bend (9 years), 5=Hock Slough (11 years), 6=Onumtuk/Emperor Bend (9 years).

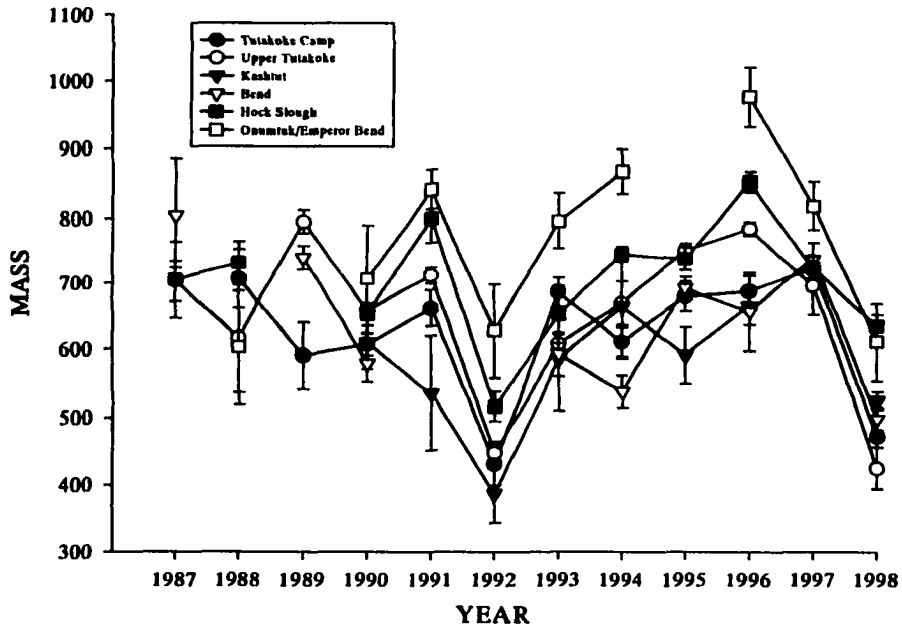

Figure 2.2. Variation in gosling growth (grams) of black brant goslings among brood-rearing areas and years. Because there was a brood-rearing area * year interaction we examined the slice effects (PROC MIXED) of both year and brood-rearing area. In years 1987 (P=0.4477), 1988 (P=0.3254), and 1997 (P=0.1039), brood-rearing areas did not differ from each other. In all other years, at least 1 brood-rearing area was significantly different from the others (P<0.0001). Within all brood-rearing areas, significant annual variation in gosling mass existed (P<0.0001)

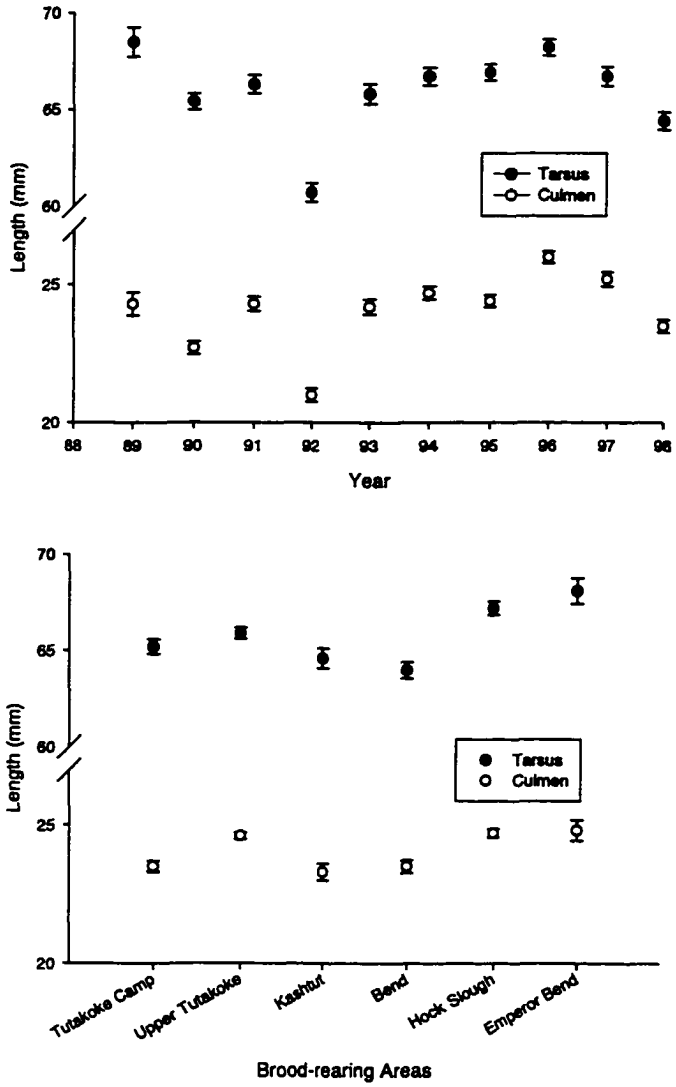

Figure 2.3. Variation in tarsus and culmen lengths (in mm) of black brant goslings among brood-rearing areas and years. Results are weighted averages of estimated least squares means and standard errors for all plausible models ($\Delta AIC_c \leq 5$). Open circles are culmen measurements and closed circles are tarsus measurements.

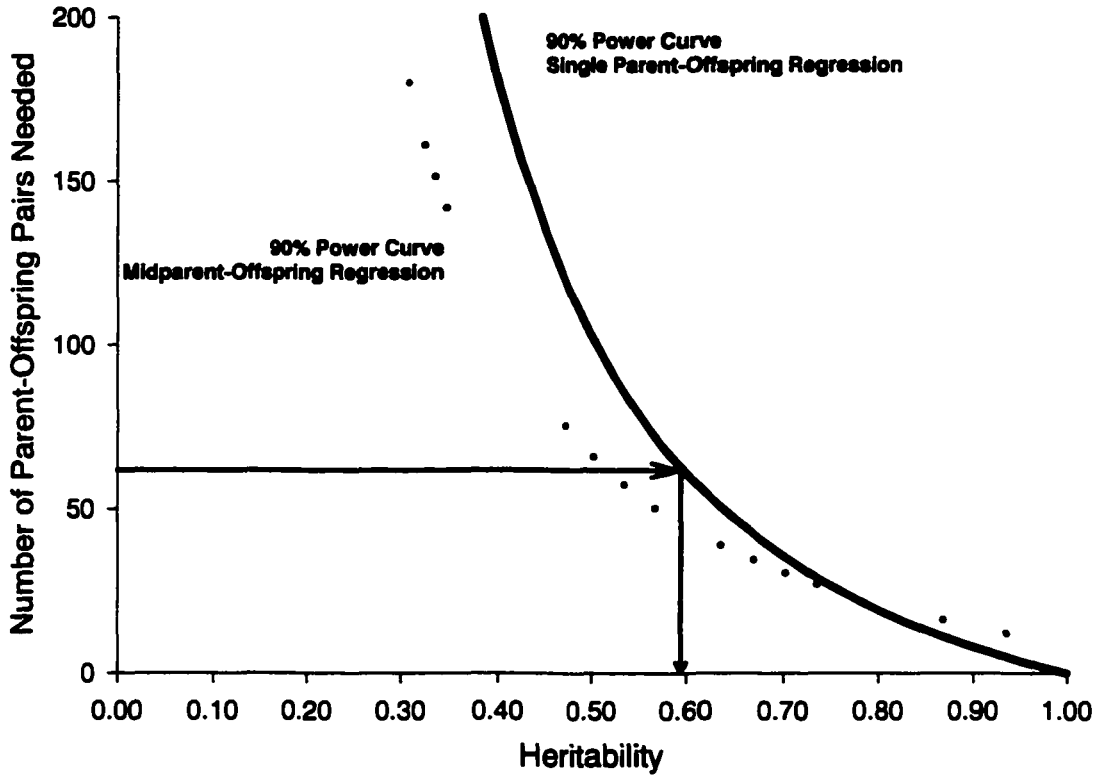

Figure 2.4. Power curve analysis for heritability estimation. Each curve represents the sample size of parent-offspring pairs needed in order to have a 90% probability that the observed slope is significantly greater than zero ($\alpha = 0.05$). Solid line is for individual parent-offspring pairs. Dotted line is for midparent-offspring regression. Formulas found in Lynch and Walsh (1998). We have 62 paired female parent-offspring data points. Thus, we have a 90% probability of detecting an estimate of heredity that is 0.60 or greater..

Chapter 3. Dynamics of Foraging Behavior Associated with Variation in Habitat and Forage Availability in Captive Black Brant Goslings (*Branta bernicla nigricans*)

ABSTRACT

We conducted an experiment to study the effect of gosling density on food abundance and feeding behavior of Black Brant (*Branta bernicla*) goslings, in two habitat types important to Black Brant on the Yukon-Kuskokwim Delta, Alaska: (1) *Carex subspathacea* grazing lawns and (2) slough levees which contain *Triglochin palustris*. Within each habitat, we manipulated grazing pressure by allowing goslings to graze specific plots every 6, 9, or 12 days. We randomly assigned six goslings to one of six treatment groups (three grazing frequencies x two habitats). Biomass of *C. subspathacea* was higher in lightly grazed plots (grazed every 12 days) than in the heavily grazed plots (grazed every 6 days). Offtake in *C. subspathacea* was also greater in the lightly grazed plots. Within *C. subspathacea* stands, the proportion of time spent feeding varied among grazing intensities. Goslings within heavily grazed plots spent more time feeding than goslings in lightly grazed plots. Within slough levee habitat there were no differences between heavily and lightly grazed plots in either biomass or offtake of *T. palustris*. Contrary to other studies, in all treatments and habitats, percent time feeding declined as gosling mass increased. Peck rates were much lower in slough levee habitat than in grazing lawns. While the trend in peck rate over time varied among treatments and

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between habitats, during trials very early in the season we observed a reduced peck rate in the heavily grazed treatment, but only within the *C. subspathacea* grazing lawns. There was no variation in peck rate among treatments within slough levee habitat. While overall percent time feeding did not vary between the two habitats, peck rates for goslings fed on *C. subspathacea* was double the rate of goslings in slough levee. Thus, the varied growth responses between habitats to variation in grazing pressure we observed during this experiment suggest the importance of density-dependent effects on brood-rearing habitat and the resulting variation in gosling growth.

INTRODUCTION

Like all arctic geese, Black Brant (*Branta bernicla nigricans,* hereafter, "brant") are obligate herbivores during the breeding season (Owen 1980). With growing seasons less than 100 days, goslings must be able to grow rapidly and fledge (Sedinger and Raveling 1986). Because brant rely on an herbivorous diet for growth, goslings are nutrient limited while on the breeding grounds (Sedinger and Raveling 1984, Sedinger and Raveling 1990, Larsson and Forslund 1991, Cooch et al. 1991a). Plant foods are relatively low in protein and metabolizable energy (Sedinger 1984, Sedinger et al. 1992), and brant must feed a large proportion of daylight hours and select foods high in protein and low in fiber (Sedinger and Raveling 1988). Because colonial geese feed at high densities, they have the potential to reduce availability of the highest quality food (Cargill and Jefferies 1984, Sedinger and Raveling 1986, Gauthier et al. 1995, Person et al. 1998). With increased brood densities and decreased forage availability, goslings must increase

time spent feeding to compensate for increased search time and maintain growth rates (Sedinger and Raveling 1988, Sedinger et al. 1995).

Food quality and availability regulate gosling growth (Sedinger and Raveling 1984, Sedinger et al. 2001) and density dependent effects on gosling growth exist in several populations of arctic geese (Larsson and Forslund 1991, Cooch et al. 1991b, Loonen et al. 1997, Black et al. 1997, Sedinger et al. 1998). Limitations in growth permanently affect early survival, adult body size and fecundity (Davies et al. 1988, Alisauskas and Ankney 1990, Cooch et al. 1992, Sedinger et al. 1995, Choudhury et al. 1996, van der Jeugd and Larsson 1998). Thus, reduced availability of high quality forage can influence life history traits.

Broods also impact food abundance (Cargill and Jefferies 1984, Sedinger and Raveling 1986, Kerbes et al. 1990, Hik et al. 1991, Gauthier et al. 1995, Person et al. 1998). While intense grazing by geese has been shown to have deleterious results (Kerbes et al. 1990), in many studies broods have been shown to maintain or improve productivity of the plants. Grazing by geese may maintain primary productivity later during the season when plants would otherwise stop producing additional above ground biomass (Cargill and Jefferies 1984), but without time for recovery late in the season this grazing may affect subsequent years growth (Hik et al. 1991). Grazing by brant broods helps maintain *Carex subspathacea* grazing lawns, that without grazing pressure would revert to a longer growth form not conducive to grazing by goslings in subsequent years (Person et al. 1998, Person et al. In press). Similarly, *Triglochin palustris* may benefit from grazing by brant, if the grazing coincides with grazing of other neighbor plants that

would otherwise compete with *T. palustris* for light and nutrients. (Mulder et al. 1996, Mulder and Ruess 1998)

Studies of brood behavior (Sedinger and Raveling 1988, Sedinger et al. 1995, Fowler and Ely 1997) have suggested that variation in time spent feeding is linked to variation in forage availability, arguing that goslings must compensate for lower forage available by increasing feeding time. No studies, however, have experimentally tested how variation in availability of forage affects feeding behavior in goslings.

To decouple variation associated with hatch date (Sedinger and Flint 1991, Cooch et al. 1991a), parental quality (Finney and Cooke 1978, Brinkhof et al. 1993, Herzog 2002), and spatial variation in forage quality (Larsson and Forslund 1991, Person et al. 1998, Sedinger et al. 2001, Herzog 2002), we performed a controlled experiment in 1994 to examine effects of brood density on vegetation and to correlate variation in forage availability with changes in foraging behavior of brant goslings in two preferred habitats.

Brant broods feed in two major habitats, *C. subspathacea* dominated grazing lawns, and grass-sedge dominated slough levee (Sedinger unpublished). Brant spend a disproportionate amount of time within *C. subspathacea* grazing lawns relative to their availability (Person and Sedinger unpublished) and *C. subspathacea* is probably a preferred forage species for brant during the breeding season. Slough levee habitat contains *T. palustris*, a small plant, previously shown to be high in nitrogen relative to other forage species, preferred by geese on the Yukon-Kuskokwim Delta (Sedinger and Raveling 1986) but low in overall biomass (Mulder et al. 1996, Jorgenson 2000) The brood-rearing habitats used by individuals from the Tutakoke brant colony vary

considerably both in brood density and vegetative composition (Person et al. 1998, Herzog 2002). Considerable variation in gosling growth is observed among brood-rearing habitats, as well (Herzog 2002).

We performed an experiment to examine the relationship between availability of *C. subspathacea* and *T. palustris*, and foraging behavior of brant goslings in the two major habitats used for foraging: *C. subspathacea* grazing lawns and slough levees. We manipulated grazing frequency to influence abundance of the two major food plants and recorded behavior of brant goslings in experimental plots.

METHODS

This research was performed at the Tutakoke River Brant Colony on the Yukon-Kuskokwim Delta, Alaska (61°N, 165°W). Detailed descriptions of the study area can be found in Sedinger et al. (1993) and Sedinger et al. (1998). The experiment was performed in 2 separate habitat types: *C. subspathacea* dominated grazing lawns, and slough levee (a mixed sedge, grass, forb community which also contains *Triglochin palustris*, a preferred food for brant).

Treatment Design.- The study design for this experiment consisted of 18, 21m^2 (3 x 7m) plots (nine in *C. subspathacea* grazing lawns, and nine in slough levee). We randomly assigned each of these plots to one of three possible grazing intensities. We established four low grazing intensity plots, three medium grazing intensity plots, and two high-intensity grazing plots (Fig. 1). Plots were enclosed using 1m tall plastic netting. Grazing pressure for the heavy, medium, and light grazing plots was accomplished by placing a group of six goslings on each plot for a total of eight hours,

every six, nine, and 12 days respectively. We used 36 goslings (two habitats x three treatments x six goslings) for this experiment.

We collected the 36 goslings at hatch on June 16, 1994 from 36 randomly selected nests. Thus, each gosling originated from a unique nest. We marked all goslings with unique combinations of colored plastic tarsal bands. We placed goslings into groups of six which were each permanently associated with one of the three treatment levels, within each of the two habitats.

To achieve the desired grazing intensity levels, each group of six goslings was placed in a plot every three days for a total of eight hours. Because each group of goslings was placed in a plot every three days, and grazing treatment levels on plots varied from six to 12 days, the number of plots within each treatment was different. Two plots were assigned to the heaviest grazing treatment. Thus, each heavily-grazed plot was grazed every sixth day. Similarly, three plots were assigned to the medium grazing treatment and four plots to the least grazed treatment, resulting in plots that were grazed every nine and 12 days respectively (Fig. 1). At all other daylight times, we allowed goslings to range freely and feed on natural vegetation within large (10 x 10 m) exclosures that were moved regularly. Gosling diets were supplemented with duck chow. During inclement weather goslings were kept in a structure where they could be out of the rain.

Measurements: Vegetation: C. subspathacea.- To estimate the amount of forage available to goslings during a treatment, we removed three 10 x 10 cm turves from each plot before goslings were placed on a plot, at mid-treatment (after 4 hours), and after

goslings were removed (8 hours). All aboveground biomass was clipped to ground surface within 24 hours of harvest, washed in fresh water and dried at 60° C in a field laboratory. These samples were later re-dried and weighed at the University of Alaska, Fairbanks. We placed the sampled turves back into each plot after clipping. Offtake of biomass by goslings was calculated as the difference between the average biomass measured before and after a given portion of the treatment, e.g. first four hours. Because biomass of *C. subspathacea* was measured pre, mid, and post trial, we calculated offtake twice for each trial (mid-pre and post-mid). Total overall offtake was also calculated as the sum of offtake during the two, four-hour periods (post-pre).

Measurements: Vegetation: Slough levee.- Slough levee plots were also sampled pre, mid, and post-treatment to estimate available biomass of *T. palustris*. During each sampling event, five 10 x 10 cm quadrats were randomly placed within the plot. Within each quadrat, we counted the total number of *T. palustris* plants, and recorded the state (grazed or ungrazed) and leaf length for each of the first 10 *T. palustris* plants sampled. Weight of each plant was calculated later, using a length-weight regression based on the length and weight of individual leaves from a previously sampled collection of *T. palustris* plants in the same area (Mulder unpubl. data). We used mean length of measured leaves to estimate length and biomass of all leaves on plots. Offtake was calculated as the difference in biomass estimates at the beginning and end of each four hour period (mid-pre and post-mid). To control for possible interactions of *T. palustris* with other plants in the community (Mulder and Ruess 1998), we measured percent cover of several species of plants as well as bare ground. Percent cover was determined by

centering a 1 x 1m quadrat on each of the smaller 10 x 10cm quadrats used to estimate *T. palustris* abundance and visually calculating percentage cover of plant species with the larger quadrat. *Potentilla egedii*, specifically, may be an important alternate forage species for black brant in the slough levee community (Sedinger pers. obs.) Therefore, we also counted the total number of grazed and ungrazed *P. egedii* plants within each 10x10cm quadrat.

Measurements: Gosling behavior.- During each eight-hour treatment, gosling behavior was recorded four times (every two hours). We recorded gosling behavior using methods described by Sedinger et al. (1995). We recorded the behavior of each individual gosling within the plot each minute for a total of one hour. Behaviors were initially grouped into specific activities (Sedinger and Raveling 1988, Welsh and Sedinger 1990, Sedinger and Raveling 1990) which were subsequently reclassified as either feeding, or not feeding for this study. During these activity budgets, feeding included searching for food and pecking for food items.

We defined peck rate as the number of pecks per second made on vegetation by a gosling, in which the gosling was continuously feeding or searching for food without any head-up postures (Sedinger and Raveling 1988). We recorded peck rates by counting the number of pecks during a period of continuous head down posture which was timed with a stop watch. Only observations that were at least 20 seconds in duration (mean=22 secs; s.d.=2.67; max=33) were included in the analysis.

Statistical Methods.- We used general linear mixed models (SAS, Proc Mixed) for all analyses (Littell et al. 1996, SAS Institute 2001). Table 1 summarizes all

statistical analyses performed. Because measurement methods were different for each habitat, analyses of offtake and biomass of plant species were performed separately for each habitat. These analyses were repeated measures, with date as the repeated factor and plot nested within treatment as a random effect. In addition, for biomass models, sample nested within plot was included as a random effect. Fixed effects, for available biomass models, included treatment level and a categorical variable used to designate whether a sample was taken before, half-way through, or after a treatment.

For each offtake model, sample nested within plot and plot nested within treatment were included as random effects with date a repeated factor. The only main effect included was treatment and initial biomass of vegetation was included as a covariate.

Estimates of *T. palustris* in slough levee biomass included variances associated with the length-weight regression, and thus *T. palustris* biomass estimates were weighted by the inverse of the variance (Neter et al. 1990). This analysis was also a repeated measures design with date as the repeated factor. Again, plot nested within treatment was included as a random effect.

For gosling behavior, our specific interest was not in whether a specific grazing treatment level affected behavior, but rather how gosling foraging behavior varied with variation in forage availability. Because there was considerable variation in available forage within treatments, we included both date and forage availability in the analysis and excluded treatment as a fixed effect. This analysis was also a repeated measures design with gosling nested within treatment as the experimental unit. Forage availability within

plots declined substantially during trials. In most cases, estimates of biomass during the second half of a trial were below levels found in the wild. Because our goal was to examine gosling behavior within an environment that approximated the natural grazing system we therefore restricted the analysis to gosling behavior data gathered during the first half of each trial.

Peck rate analysis was performed with a similar repeated measures design. Fixed effects included habitat, treatment, and time of day. Plot nested within treatment was included as a random effect.

We used information-theoretic methods for model selection (Burnham and Anderson 1998). We included in the set of candidate models, all models with any combination of fixed effects, 2-way interactions, as well as 3-way interactions that incorporated a covariate. More complicated models were not biologically interpretable or statistically manageable. Akaike's Information Criteria, corrected for small sample size (AIC_c), was calculated for each model. The model with the smallest AIC_c, as well as all models within four AIC_c points, were included in the final model set (Burnham and Anderson 1998). Parameter estimates were calculated by model averaging the estimated least squares means from all models in the final model set (Anderson et al. 2000). Unconditional variances were estimated similarly (Anderson et al. 2000).

RESULTS

C. subspathacea plant results.- Biomass of *C. subspathacea* before trials, decreased throughout the experiment in all treatments (Table 2, Fig. 2). While always less than before trials, measurements of *C. subspathacea* biomass halfway through trials

increased with date. Finally, post-trial biomass did not change for the lightly or medium grazed treatments, while biomass in the heavily-grazed treatment decreased by almost 50% during the experiment (Fig. 2).

After controlling for date, the biomass of *C. subspathacea* was significantly greater in the lightly-grazed treatment throughout the experiment. In general, there was no difference in biomass between the medium and heavily grazed treatments (Fig. 2).

For *C. subspathacea* offtake during the first 4 hours ($offtake_{1,2}$), a model which included only initial *C. subspathacea* biomass had the lowest AIC_c score (Table 2; slope = 0.2663 ± 0.04371 g offtake per g available biomass). A second model which included initial biomass of *C. subspathacea* and date was less likely (Table 2), and the date effect very minimal (-0.00017 ± 0.00018 change in offtake (g) of *C. subspathacea* per day). The model for offtake of *C. subspathacea* during the second half of trials was similar. The most likely model given the data included only *C. subspathacea* biomass measured at midpoint of treatment as a main effect (Table 2; slope=0.219 ± 0.0414 g offtake per g available biomass).

Slough levee plant results.- T. palustris biomass in slough levee was dependent on date and when during trials it was measured (Table 2). The most likely model suggested a decrease in biomass of *T. palustris* throughout the experiment. In addition, there was significantly less biomass after trials than before (Fig. 3).

The most likely model for offtake of *T. palustris,* during the first 4 hours of trials included initial *T. palustris* biomass (slope=0.512 ± 0.212 g offtake per g available biomass) as a main effect. However a model with date (slope=0.00051 ± 0.000316 g

increase in offtake per day) as a covariate was nearly as likely (Table 2). During the second four hours of trials, the most likely model for offtake of *T. palustris* included only an estimate of the intercept, suggesting little variation existed in offtake of *T. palustris* during the second four hours (Table 2).

We modeled *P. egedii* results separately to examine the plant species response to feeding by goslings. The most likely model for both total number of *P. egedii* (grazed and ungrazed), as well as the number of grazed *P. egedii* included both effects of treatment and time of sampling within trials as fixed factors (Table 2). In addition, the most likely model for the total number of *P. egedii* plants (grazed and ungrazed) suggested the total number of *P. egedii* plants increased during the summer. For total number of grazed *P. egedii*, the final model included the total number of grazed and ungrazed *P. egedii*. There were significantly fewer *P. egedii* plants within heavily-grazed plots than other plots, and significantly fewer grazed *P. egedii* within the lightly-grazed plots than other plots. Also, there were significantly more total *P.egedii* plants before trials than after, and there were more grazed *P. egedii* plants after a trial than before goslings were placed on plots (Table 3).

Gosling Behavior.- In *C. subspathacea* grazing lawns, percentage of time spent feeding declined with increasing date and increased biomass of *C. subspathacea*. The most likely model also included a positive interaction between date and available forage (Table 2; Fig. 4). In slough levee habitat, similar relationships between date, biomass of *T. palustris* available, and percent time feeding existed (Fig. 5). The percent time feeding by goslings was negatively correlated with date (-1.1 % ± 0.2 per day).

Estimates of peck rates within *C. subspathacea* grazing lawns were more than double estimates within the slough levee habitat. In the most likely model, the only significant variation in peck rates among treatments was within the *C. subspathacea* grazing lawns (Fig. 6). During trials early in the summer, goslings within the lightly-grazed plots of *C. subspathacea* pecked less than those in heavily grazed plots. However, during trials later in the season there were no differences in peck rate among treatments within the *C. subspathacea* community.

DISCUSSION

Forage biomass – comparison of conditions created by treatments and that observed in wild.- Our estimates of forage biomass in all treatments and habitats were comparable to those observed in the wild. Within *C. subspathacea* grazing lawns forage biomass varied initially from 30 – 45 g/m^2 and declined throughout the study to final estimates of 15 – 40 g/m^2. During the same year as this study, Person et al. (1998) observed variation in standing crop biomass from 17.8 - 52.2 g/m^2 (early in season during nesting) and 17.8 – 80.6 g/m^2 (in late brood rearing). In general, Person et al. (1998) measured no change or a slight increase in standing crop biomass as the season progressed, whereas we found declining biomass in all experimental grazing treatments as the season progressed. These results suggest our simulated grazing treatments may not represent brood-rearing areas with light grazing pressure, but do represent those areas that experienced high grazing pressures. Alternatively, treatments may have been less productive than the plots measured by Person et al. (1998). However, Person et al.

(1998) found no spatial variation in productivity for plots within the same year and location as our treatment plots.

Within the slough levee habitat, our measures of *T. palustris* biomass are comparable to those observed in the wild (this experiment: 2 – 4 g/m^2; B.T. Person, unpubl.(1994): 2 – 4 g/m^2; Herzog unpublished (1996-1998): 2 – 3 g/m^2).

Forage biomass dynamics in C. subspathacea grazing lawns and slough levee habitat.- Within *C. subspathacea* grazing lawns, all grazing treatments reduced forage biomass. During trials early in the summer, total biomass of *C. subspathacea* was reduced by 50% in the first four hours with very little offtake in the second four hours (Fig. 2). The disproportionate reduction in *C. subspathacea* during the first four hours of each trial compared to the second four hours likely represents the declining foraging efficiency of goslings as biomass declined below 25 g/m^2. Because *C. subspathacea* occurs in continuous, monospecific stands, the ability of goslings to remove pieces of leaf likely limits intake.

In slough levee habitat, *T. palustris* biomass decreased during the experiment. In addition, we did not observe a difference in available biomass of *T. palustris* among the three grazing treatments, even though the more heavily grazed treatments had only six days to recover between grazing events, rather than the 12 days for the lightly grazed treatment. Lack of variation in biomass among grazing treatments implies production of *T. palustris* within the heavily grazed treatment was higher than in the lightly grazed treatment. Mulder et al. (1996) and Mulder and Ruess (2001) suggest that a complex interaction between species competition and gosling selectivity plays an important role in

T. palustris availability. If goslings are highly selective for *T. palustris,* grazing may substantially reduce availability of *T. palustris*. However, if goslings also feed on or trample other forage plants that compete with *T. palustris* for light and nutrients, foraging activity may increase productivity of *T. palustris*, partially compensating for grazing (Mulder pers. comm.).

Similar to *C. subspathacea* grazing lawns, 70 – 100% of the offtake of *T. palustris* occurred within the first four hours of trials (Fig. 3). These data suggest that within the slough levee plots, biomass of *T. palustris* after four hours of grazing, is sufficiently reduced so geese cannot feed efficiently. Mulder and Ruess (1998) found the presence of neighboring individual plants reduced the probability that *T. palustris* individuals would be grazed, likely because these other plants reduced detection of *T. palustris* individuals. Thus, the inability of goslings to reduce biomass of *T. palustris* in the second four hours of a trial was likely a result of becoming increasingly less visible, and consequently less available.

We hypothesize that goslings were able to reduce *C. subspathacea* to the limits of their mechanical ability to graze it, typically in the first four hours of each trial. Biomass had more time to increase in the most lightly grazed treatment (grazed every 12 days), compared to the most heavily grazed treatment (grazed every six days), resulting in greater biomass in the former at the beginning of trials. Nonetheless, grazing was sufficient to reduce biomass of *C. subspathacea* during trials in all treatments over the summer. In contrast, the more sparse and patchy distribution of *T. palustris* (Mulder and Ruess 1998) limited the ability of goslings to rapidly consume plant biomass. Instead,

interactions between protection and competition with neighboring plant species generated variation in biomass production within the heavily and lightly grazed slough levee plots.

Variation in gosling foraging behavior.- Peck rates in the *C. subspathacea* grazing lawns were almost double those observed in slough levee, which is attributable to the different feeding tactics required in the two habitats. Within the grazing lawns, vegetation is uniform, and little searching is required. Food intake is primarily limited by the sizes of leaves and maximal pecking rate. However, *T. palustris* is clumped and variable in distribution, and shielded by surrounding vegetation (Mulder and Ruess 1998), which requires goslings to spend more time searching for food during foraging bouts within the slough levee habitat.

Proportion of time spent feeding during this experiment (estimated least squares range: 0.34 – 0.88) is within the range of previous results from both captive and wild goslings (Sedinger and Raveling 1988, Manseau and Gauthier 1993, Sedinger et al. 1995, Fowler and Ely 1997). Unique to this experiment, however, is the lack of a positive date effect on percent time feeding compared to other studies (Sedinger and Raveling 1988, Sedinger and Raveling 1990, Sedinger et al. 1995, Fowler and Ely 1997). Instead, our results suggest that gosling behavior is influenced in a complex way by date and available forage. In experimental *C. subspathacea* grazing lawns, time spent feeding is negatively correlated with both date and forage availability, but there was also an interaction between date and forage availability (Fig. 4).

Captive goslings were fed ad-libitum when not on experimental plots and potentially were less motivated to feed when food was restricted especially toward the

end of experimental trials. Alternatively, reduced time spent feeding in response to reduced forage may have been an attempt to reduce energy expenditure when food was restricted, thereby minimizing negative effects of reduced food abundance (Schew and Ricklefs 1998). Older goslings had large lipid reserves (Herzog 2002) associated with ad libitum feeding when off treatments. Thus, reduced foraging with increasing date may have reflected the somewhat artificial state of our experimental goslings relative to those in the wild.

The interaction between date and forage availability in *C. subspathacea* was manifested in a relatively steep decline in time spent foraging with increasing date at very low forage levels, but a weak relationship between date and foraging time at higher forage abundance. Goslings in the wild typically experience standing crops > 30 g/m^2 during the middle of brood-rearing (Person et al. 1998), even under conditions in which food availability limited growth of goslings (Sedinger et al. 1998). At a standing crop of > 30 g/m^2 the relationship between foraging time and date is weak. We, therefore, expect date, by itself, to have little effect on gosling foraging behavior in the wild.

In the wild, biomass of preferred foods generally declines as brood-rearing progresses (Sedinger and Raveling 1986, Person et al. 1998) associated with grazing by broods coupled with a decline in primary productivity. Increased time spent foraging by wild goslings with advancing date has been interpreted as a response to reduced food availability (Sedinger and Raveling 1988, Sedinger et al. 1995, Fowler and Ely 1997) and the relationship between biomass of *C. subspathacea* and foraging time in experiments reported here is consistent with this hypothesis.

Within the slough levee habitat, foraging time was influenced by date, and possibly *T. palustris* biomass (Table 2). As in *C. subspathacea* grazing lawns, we believe available forage biomass is the principle determinant of foraging time within the slough levee community. However, because goslings were able to feed ad-libitum when not in a trial, goslings were not as nutrient limited as would be expected in the wild. Instead as availability dropped below a critical level, goslings shifted strategies and reduced foraging time.

In *C. subspathacea* grazing lawns, there is a negative causal link between time spent foraging and forage biomass, especially early in the season when goslings are more susceptible to low forage intake. In slough levee habitats, the relationship between foraging time and forage biomass is the converse. Within slough levee, the availability of *T. palustris* may decrease as growth of other vegetation makes it more difficult for goslings to find and feed on *T. palustris* (Mulder and Ruess 1998). While many studies have suggested that seasonal change in gosling behavior is the result of seasonal shifts in forage biomass (Sedinger and Raveling 1988, Sedinger et al. 1995, Fowler and Ely 1997), we present the first example of the causal link between forage biomass and availability, and gosling behavior.

ACKNOWLEDGMENTS

We greatly appreciate C. Mulder for providing unpublished data on *Triglochin palustris* lengths and weights. We acknowledge the field assistance of M. Eichholz, T. Obritschkewitsch, B. O'Connell, B. Person for both care of goslings and vegetative sampling. Financial support was provided by National Science Foundation grant (OPP 92

14970). Logistic and additional support provided by the Department of Biology and Institute of Arctic Biology at the University of Alaska Fairbanks. This paper benefited greatly from comments by R. Ruess, E. Rexstad, D. McGuire.

LITERATURE CITED

Alisauskas, R.T., and C.D. Ankney. 1990. Body size and fecundity in lesser snow geese. Auk 107:440-443.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.

Black, J.M., E.G. Cooch, M.J.J.E. Loonen, R.H. Drent, and M. Owen. 1997. Body size variation in barnacle goose colonies: evidence for local saturation of habitats. Pages 129-140 *in* Research on Arctic Geese (Mehlum, F., J.M. Black, and J. Madsen, Eds.). Norsk Polarinstitutt, Oslo.

Brinkhof, M.W.G., A.J. Cave, F.J. Hage, and S. Verhulst. 1993. Timing of reproduction and fledging success in the Coot *Fulica atra* - evidence for a causal relationship. Journal of Animal Ecology 62:577-587.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference : A practical information-theoretic approach. Springer, New York.

Cargill, S.M., and R.L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology 21:669-686.

Choudhury, S., J.M. Black, and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. Ibis 138:700-709.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: Evidence of environmental degradation?. Journal of Animal Ecology 60:483-496.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1992. Is there a positive relationship between body size and fecundity in lesser snow geese?. Auk 109:667-673.

Davies, J.C., R.F. Rockwell, and F. Cooke. 1988. Body-size variation and fitness components in lesser snow geese (*Chen caerulescens caerulescens*). Auk 105:639-648.

Finney, G., and F. Cooke. 1978. Reproductive habits in the snow goose: the influence of female age. Condor 80:147-158.

Fowler, A.C., and C.R. Ely. 1997. Behavior of cackling Canada geese during brood rearing. Condor 99:406-412.

Gauthier, G., R.J. Hughes, A. Reed, J. Beaulieu, and L. Rochefort. 1995. Effect of grazing by greater snow geese on the production of graminoids at an Arctic site (Bylot Island, NWT, Canada). Journal of Ecology 83:653-664.

Herzog, M.P. 2002. Environmental regulation of growth in black brant. Ph.D. Dissertation. University of Alaska Fairbanks.

Hik, D.S., H.A. Sadul, and R.L. Jefferies. 1991. Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. Journal of Ecology 79:715-730.

Jorgenson, M.T. 2000. Hierarchial organization of ecosystems at multiple spatial scales on the Yukon-Kuskokwim Delta, Alaska, USA. Arctic Antarctic and Alpine Research 32 :221-239.

Kerbes, R.H., P.M. Kotanen, and R.L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: A keystone species on the west coast of Hudson Bay. Journal of Applied Ecology 27:242-258.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619-636.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.

Loonen, M.J.J.E., K. Oosterbeek, and R.H. Drent. 1997. Variation in growth of young and adult size in Barnacle Geese *Branta leucopsis*: evidence for density dependence. Ardea 85:177-191.

Manseau, M., and G. Gauthier. 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74:2045-2055.

Mulder, C.P.H., and R.W. Ruess. 1998. Effects of herbivory on arrowgrass: Interactions between geese, neighboring plants, and abiotic factors. Ecological Monographs 68:275-293.

Mulder, C.P.H., and R.W. Ruess. 2001. Long-term effects of changes in goose grazing intensity on arrowgrass populations: a spatially explicit model. Journal of Ecology 89:406-417.

Mulder, C.P.H., R.W. Ruess, and J.S. Sedinger. 1996. effects of environmental manipulations on *Triglochin palustris*: implications for the role of goose herbivory in controlling its distribution. Journal of Ecology 84:267-278.

Neter, J., W. Wasserman, and M.H. Kutner. 1990. Applied linear statistical models, 3rd Edition. Richard D. Irwin, Inc.,

Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd, London.

Person, B.T., C.A. Babcock, and R.W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific black brant geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243-259.

SAS Institute. 2001. The SAS System for Windows. Version: 8.2.

Schew, W.A., and R.E. Ricklefs. 1998. Developmental Plasticity. Pages 288-304 *in* Avian growth and development: Evolution within the altricial-precocial spectrum (Starck, J.M. and R.E. Ricklefs, Eds.). Oxford University Press, New York.

Sedinger, J.S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management 48:1128-1136.

Sedinger, J.S., M.W. Eichholz, and P.L. Flint. 1995. Variation in brood behavior of black brant. Condor 97:107-115.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger, J.S., M.S. Lindberg, B.T. Person, M.W. Eichholz, M.P. Herzog, and P.L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J.S., and D.G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger, J.S., and D.G. Raveling. 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55:1083-1102.

Sedinger, J.S., and D.G. Raveling. 1990. Parental behavior of cackling Canada geese during brood rearing: Division of labor within pairs. Condor 92:174-181.

Sedinger, J.S., M.P. Herzog, B.T. Person, M.T. Kirk, T. Obritschkewitsch, P.P. Martin, and B.A. Anderson. 2001. Large scale variation in growth of black brant goslings related to food availability. Auk 118:1088-1095.

Sedinger, J.S., C.J. Lensink, D.H. Ward, R.M. Anthony, M.L. Wege, and G.V. Byrd. 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. Wildfowl 44:49-59.

Sedinger, J.S., and D.G. Raveling. 1988. Foraging behavior of cackling Canada Goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

Sedinger, J.S., R.G. White, and W.E. Hauer. 1992. Heat increment of feeding and partitioning of dietary energy in yearling Black Brant. Canadian Journal of Zoology 70:1047-1051.

van der Jeugd, H.P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67:953-966.

Welsh, D., and J.S. Sedinger. 1990. Extra-pair copulations in black brant. Condor 92:242-244.

Table 3.1. Description of all models tested for each response variable. All variables marked with an X indicate the variable was included in the most general model. Akaike's Information Criteria, corrected for small sample size (AIC_c) were calculated for all models which are subsets of the general model

Response	Main Effects and Covariates										Interactions		Random Effects	
	HAB	TRT	BUDNO	PREPST	DAY	MASS	GOS	FORAVAIL	NO_POTENT	NO_POTENT_GR	ALL	2WAY+C	PLOT(TMT)	SAMPLE(PLOT)
***Carex subspathaces* grazing lawns**														
Biomass		X		X	X		X				X		X	X
Offtake		X		X	X	X	X				X		X	
Slough levee habitat														
Biomass		X		X	X		X		X	X	X		X	X
Offtake		X		X	X	X	X				X		X	
No_potent		X		X	X		X							
No_potent_gr		X		X	X		X		X		X		X	X
Black brant goslings														
Behavior					X		X	X				X	X	
Peckrate	X	X	X		X	X	X					X	X	

Abbreviations: HAB = Habitat, TRT=Grazing intensity treatment, BUDNO = Time budget during which data was taken, PREPST = whether samples were collected before, half way (after 4 hours), or at the end of a treatment, DAY = julian date of sample, MASS = initial mass of either goslings (for brant analyses) or vegetation (for offtake analyses), GOS = number of goslings within plot during treatment, NO_POTENT = number of *Potentilla egedii* plants counted within sample, NO_POTENT_GR = number of grazed *Potentilla egedii* plants counted within sample, ALL = All possible interactions were included in most general model, 2WAY+C = all possible 2-way interactions as well as 2-way interactions plus a covariate were included in most general model, PLOT(TMT) = plot nested within treatment included as a random effect, SAMPLE(PLOT) = sample nested within plot included as a random effect.

Table 3.2. Results from model selection for all mixed model analyses on vegetation biomass and gosling behavior. The best fit models, and all potential alternate models ($\Delta AIC_c \leq 3$) are presented.

Response Variables	Main effects and covariates	AIC_c	ΔAIC_c
Carex subspathacea			
BIOMASS			
	TMT, PREPOST, TMT*PREPOST, DATE*TMT, DATE*PREPOST	-438.8	0.0
	TMT, PREPOST, TMT*PREPOST, DATE, DATE*TMT, DATE*PREPOST	-436.4	2.4
	TMT, PREPOST, TMT*PREPOST, DATE*PREPOST	-435.8	3.0
OFFTAKE (1st 4 hours)			
	MASS	-48.1	0.0
	MASS, DAY	-46.0	2.1
OFFTAKE (2nd 4 hours)			
	MASS	-53.6	0.0
Slough levee habitat			
BIOMASS			
	PREPOST, DAY PREPOST*DAY	-1886.0	
	TMT, PREPOST, DAY, PREPOST*DAY	-1885.6	0.4
OFFTAKE (1st 4 hours)			
	MASS	-104.1	
	MASS, DAY	-102.7	1.4
OFFTAKE (2nd 4 hours)			
	INTERCEPT ONLY	-77.8	
Number of *Potentilla* Plants			
	PREPOST,DAY	1129.1	0.0
	TMT,PREPOST,DAY	1129.3	0.2
Number of grazed *Potentilla*			
	PREPOST, NO_POTENT	414.0	0.0
Black brant goslings			
PCT. TIME FEEDING			
Carex subspathacea	FORAVAIL, DAY, FORAVAIL*DAY	89.5	0.0
Slough Levee	DAY	73.5	0.0
	FORAVAIL, DAY	75.6	2.1
PECK RATE			
	HAB, TMT, HAB*TMT, TMT*DAY, HAB*TMT*DAY	1147.9	0.0

Abbreviations: HAB=Habitat, TMT=Grazing intensity treatment, BUDNO=Time budget during which data was taken, PREPOST=whether samples were collected before, half way (after 4 hours), or at the end of a treatment, DAY=julian date of sample, MASS= initial mass of either goslings (for brant analyses) or vegetation (for offtake analyses), NO_POTENT=number of *Potentilla egedii* plants within sample.

Table 3.3. Average number of *Potentilla egedii* within a 0.01 m^2 plot for each treatment within slough levee habitat.

Treatment	Total Number of Potentilla Plants		Number of Grazed Potentilla Plants	
	Pre Trial	Post Trial	Pre Trial	Post Trial
Grazed Every 6 days	5.0 ± 3.5	3.0 ± 2.7	0.3 ± 0.6	0.6 ± 1.1
Grazed Every 9 Days	6.5 ± 3.1	5.4 ± 3.6	0.3 ± 0.5	0.6 ± 0.7
Grazed Every 12 days	5.5 ± 3.8	6.0 ± 4.0	0.0 ± 0.2	0.2 ± 0.5

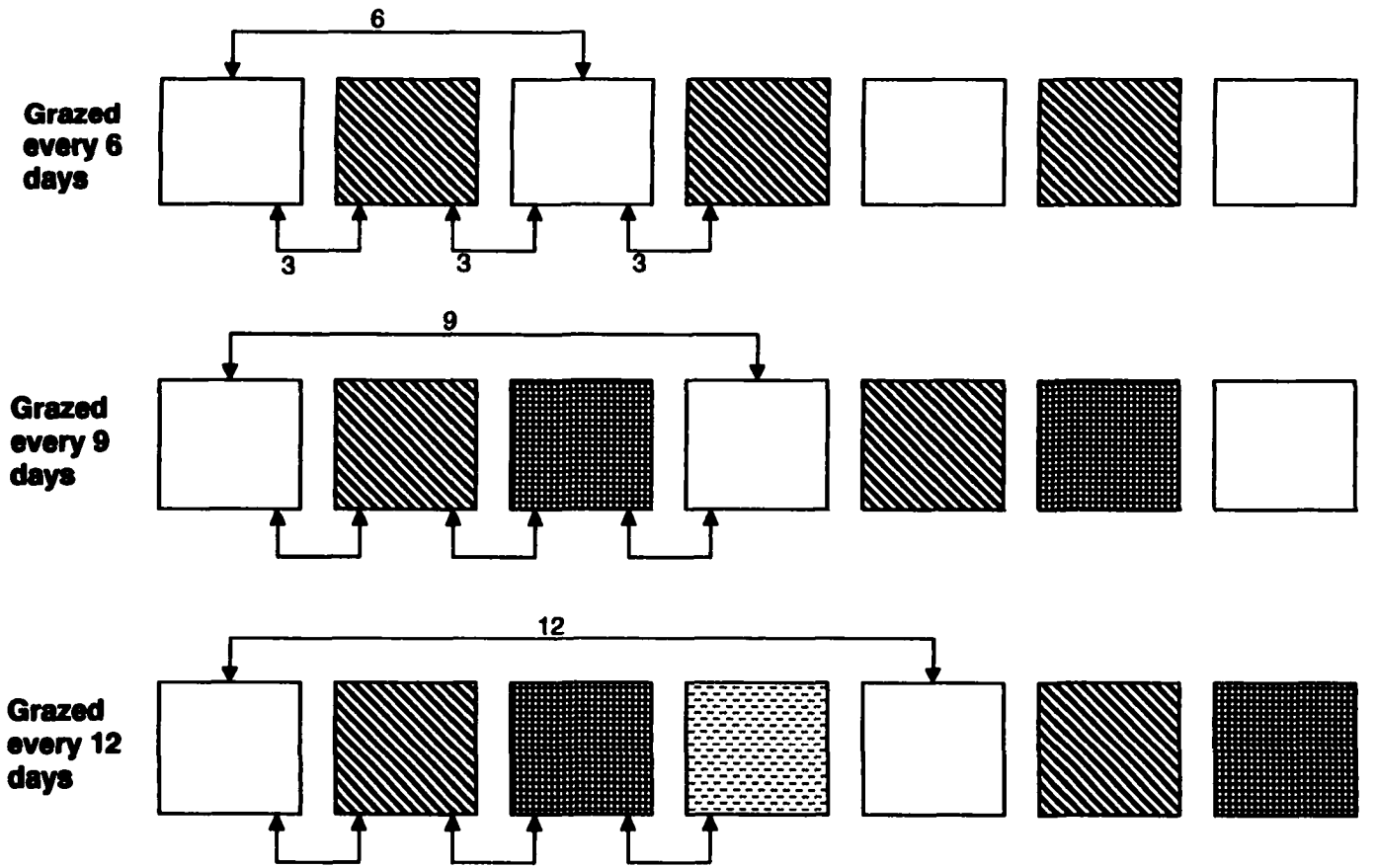

Figure 3.1. Schematic of treatment design. Goslings were assigned to a specific treatment and were placed on a plot every 3 days. In order to create variation in treatment levels, 2, 3, or 4 plots were assigned to a treatment. This created treatments in which plots were grazed either every 6, 9, or 12 days, corresponding to heavy, medium, and light grazing intensity.

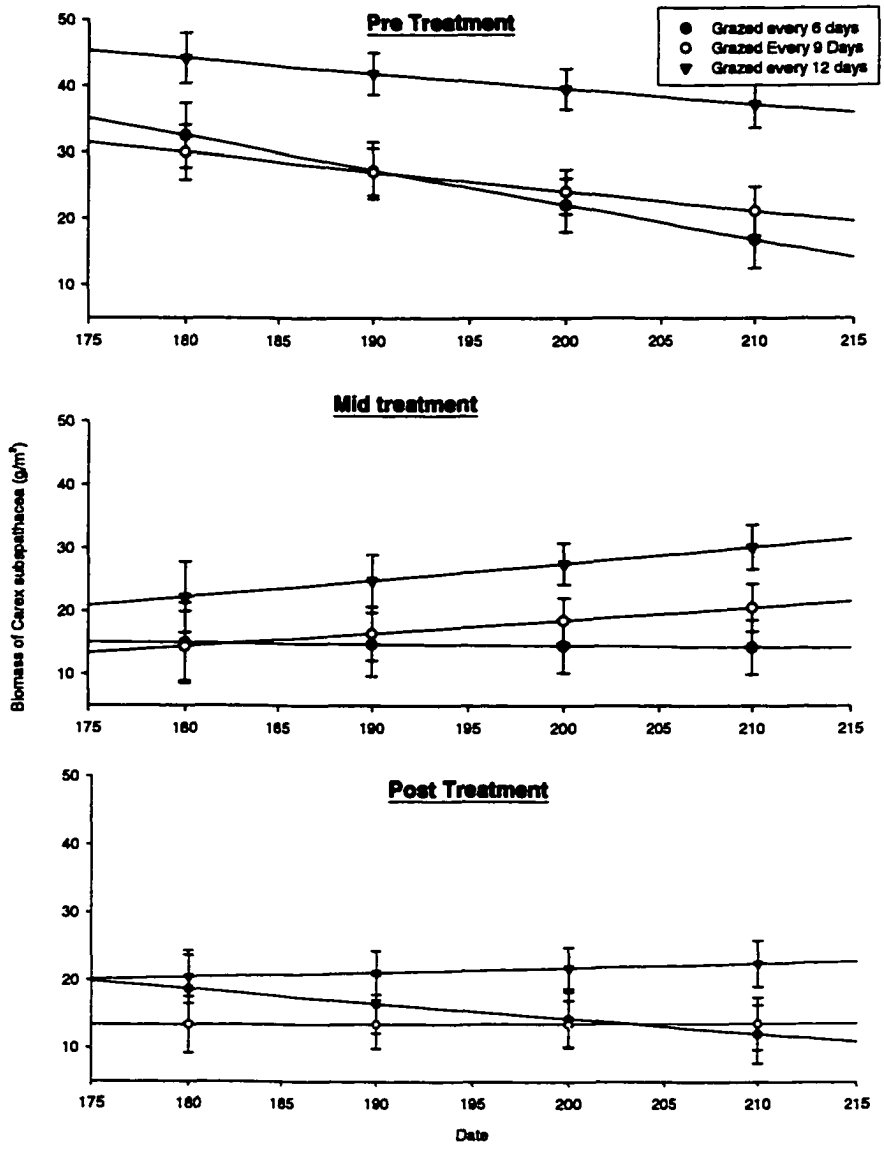

Figure 3.2. Trend in biomass over time of *Carex subspathacea* in heavily (every 6 days), medium (every 9 days) and lightly (every 12 days) grazed plots. Results presented are estimated least square means and standard errors for samples taken before, halfway (after 4 hours), and after a trial.

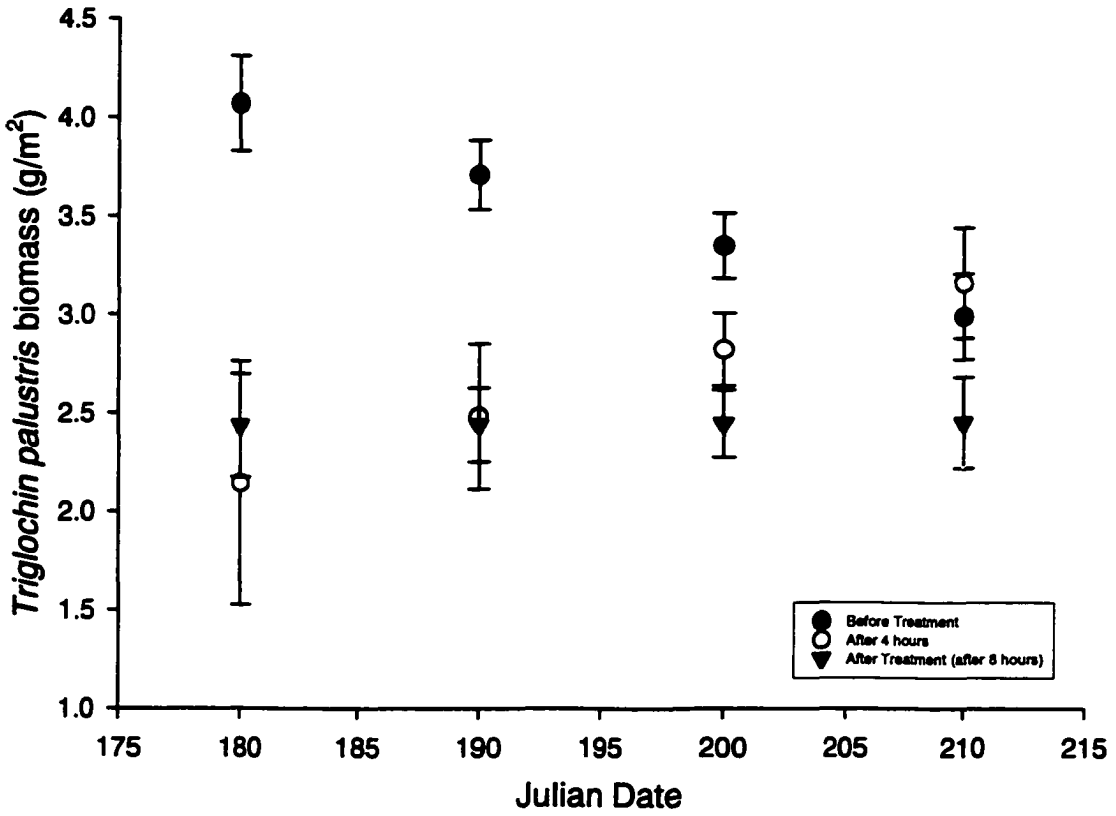

Figure 3.3. Estimated *Triglochin palustris* biomass measured before, halfway (after 4 hours), and after a trial. Results are estimated least squares and standard errors.

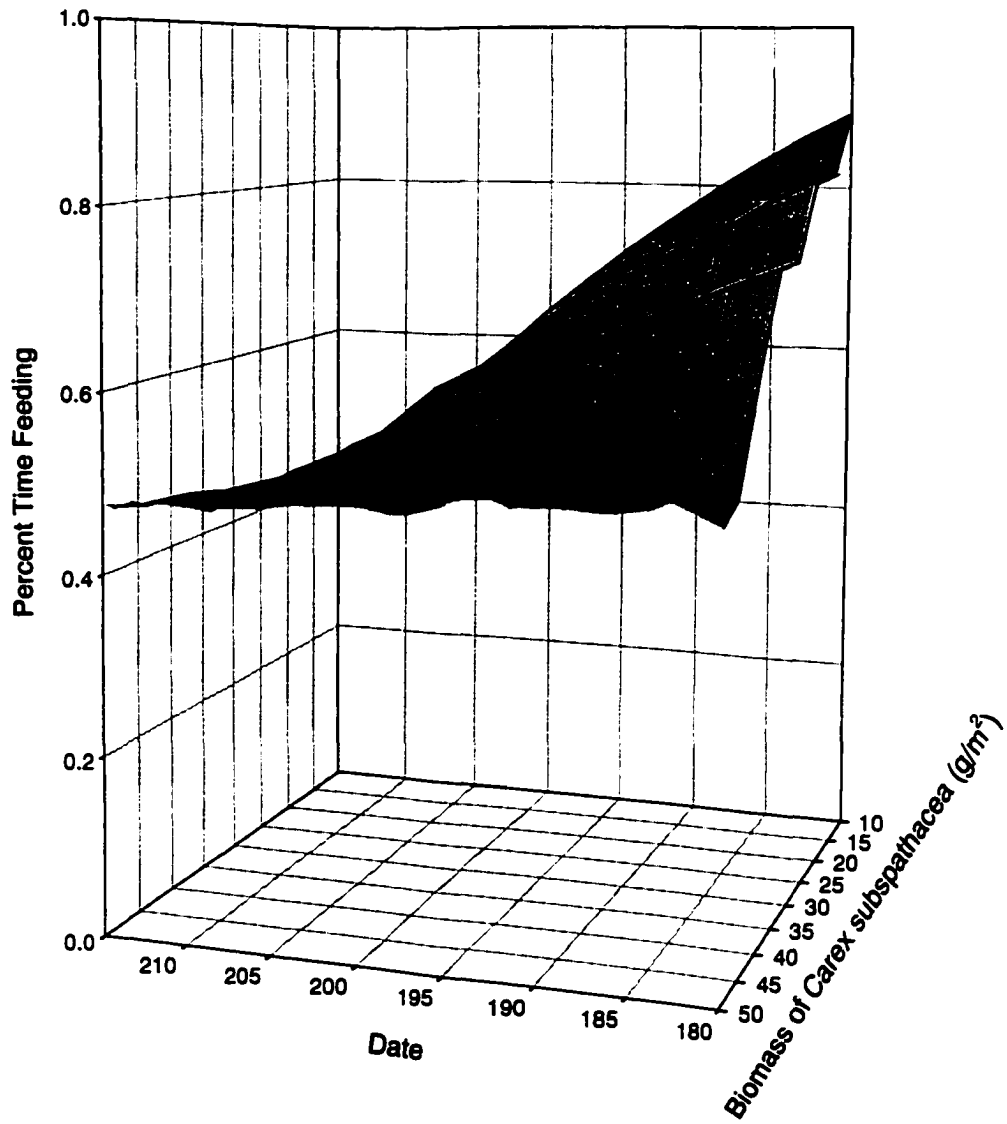

Figure 3.4. Variation in percent time feeding of black brant (*Branta bernicla*) goslings in *Carex subspathacea* grazing lawns as a function of forage available and date. Results are 3d mesh plot of equation from most likely model.

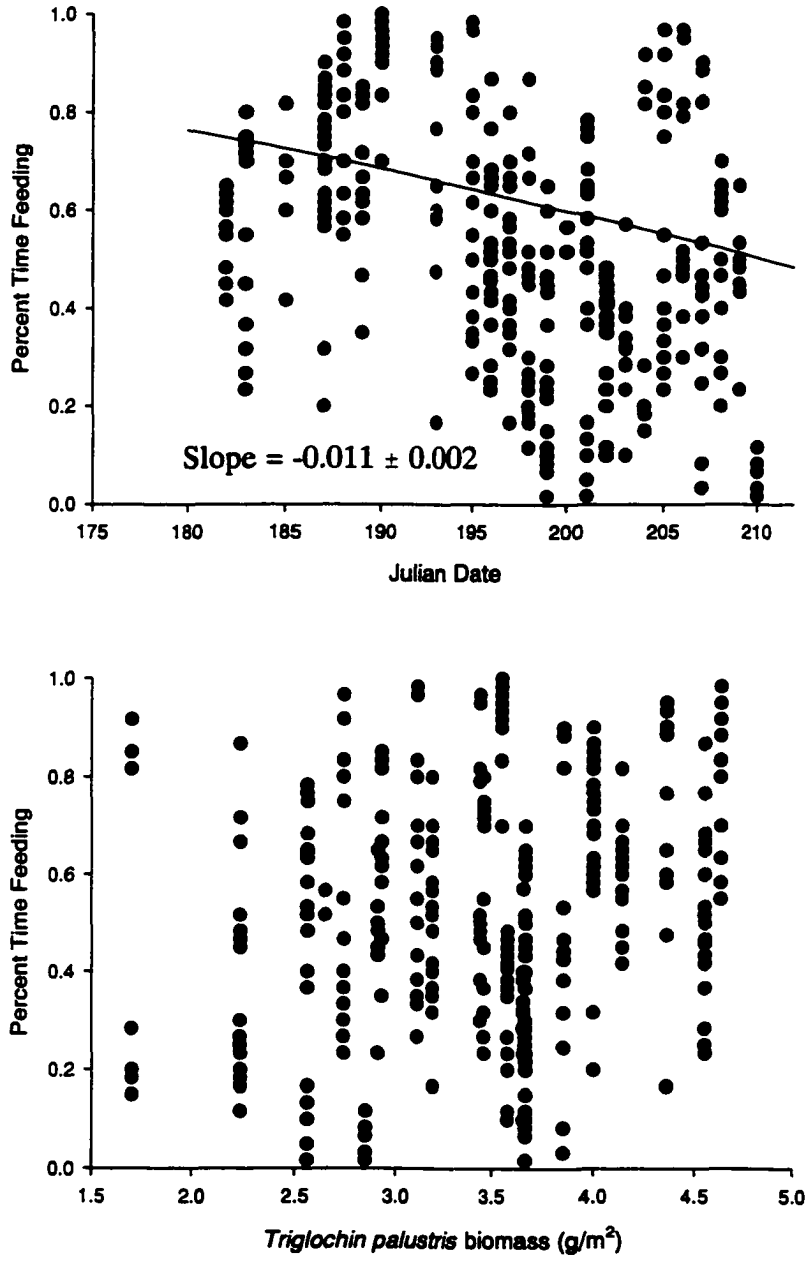

Figure 3.5 Variation in percent time feeding of Black Brant (*Branta bernicla*) goslings with respect to date and variation in *Triglochin palustris* biomass. Slope estimate is based on repeated measures analysis as described in text.

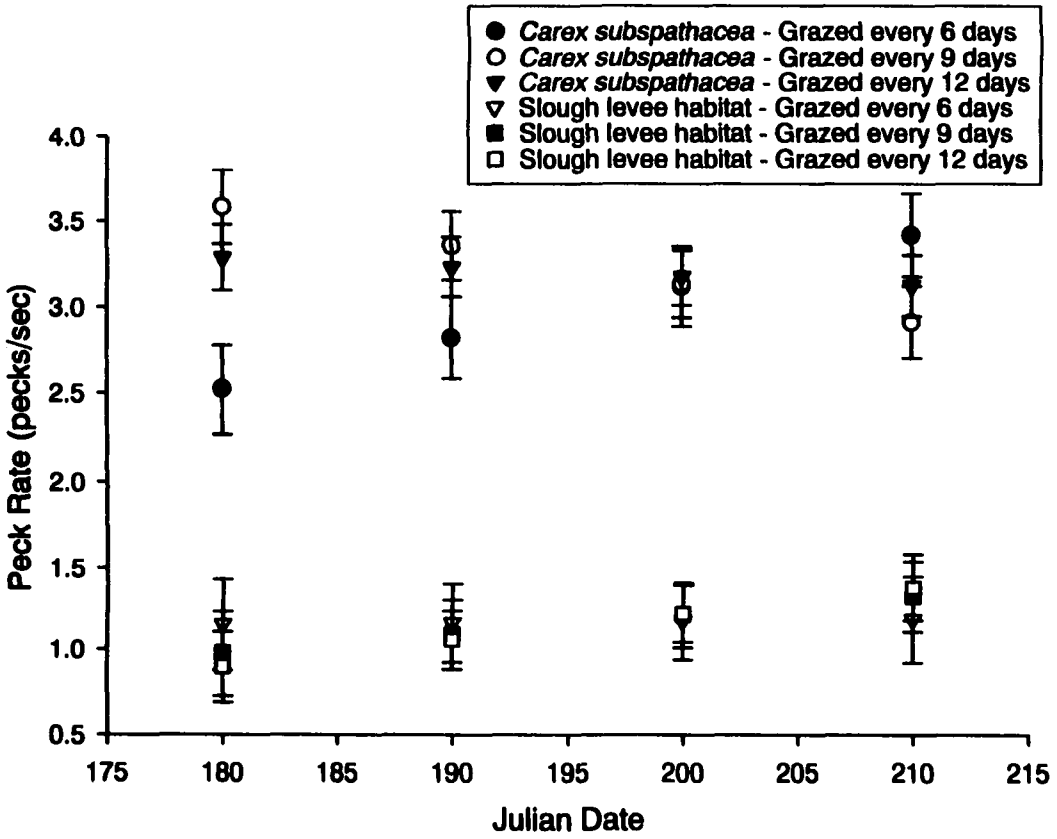

Figure 3.6. Variation in peck rate in black brant. Results are estimated least squares and standard errors for heavily (every 6 days), medium (every 9 days) and lightly (every 12 days) grazed plots in both slough levee and Carex subspathacea mudflat habitats.

Chapter 4. Dynamics of Gosling Growth Associated with Variation in Habitat and Forage Availability in Captive Black Brant Goslings (*Branta bernicla nigricans*)

ABSTRACT

Growth rates of goslings in several species of arctic geese decline in association with increased brood density. First year survival is highly correlated with gosling growth. Thus, gosling size in late summer on the Yukon-Kuskokwim (Y-K) Delta is an important determinant of black brant recruitment on the Y-K Delta. We conducted an experiment to study the effect of 3 simulated gosling density levels on gosling growth in two different habitat types used by broods from the Tutakoke River Black Brant Colony, Y-K Delta. Simulated density levels were created by allowing goslings to graze a specific plot every 6, 9, or 12 days. We placed captured goslings in one of six treatment groups (3 grazing frequencies x 2 habitats-*Carex subspathacea* grazing lawn and slough levee). Goslings remained in a specific treatment group throughout the experiment. We placed goslings in the appropriate plot and allowed them to graze for 8 hours, every 3 days. At all other times goslings were free ranging and fed ad libitum food. We found ninth primary to be longer in goslings held in *C. subspathacea* grazing lawns than in slough levee ($p<0.0001$). Change in mass over an eight hour trial was positively correlated with the amount of forage biomass in the plot at the start of the trial. We found no variation in internal morphometrics or body composition (protein, lipids, and ash) among goslings

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across any of the habitat * treatment combinations. Of all body size and structural measurements, only ninth primary varied among habitat * treatment combinations. These data are consistent with findings that correlate spatial variation in forage availability, brood numbers, and growth among brant goslings reared at Tutakoke River (Herzog 2002, Person et al. In press).

INTRODUCTION

Variation in gosling growth and size at fledging has been attributed to variation in available food, at least partially associated with local density (Lepage et al. 1998, Sedinger et al. 1998). Because size of goslings after their first summer influences first-year survival (Owen and Black 1989, Sedinger et al. 1995), final adult size (Larsson and Forslund 1991, Cooch et al. 1991a, Sedinger et al. 1995) and fecundity (Sedinger et al. 1995), it is an important determinant of their fitness and growth of goslings is a principle mechanism by which population density feeds back on population growth.

Limits on both energy acquisition and energy expenditure place constraints on energy budgets of rapidly-developing waterfowl (Weiner 1992). While high rates of growth (Sedinger 1986) require a minimum of nutrient concentration in forage to sustain rapid gosling growth (Manseau and Gauthier 1993), the relatively small body size of geese places a maximum limit on the processing rate of food in the gut (Sedinger and Raveling 1988, Sedinger 1997). This problem is exacerbated by the relatively low levels of protein and relatively high levels of cell wall in green plants, and by the imbalance of some essential amino acids in green plants, relative to tissues in growing goslings (Sedinger and Raveling 1984, Sedinger 1984, Sedinger and Raveling 1988).

Consequently, goslings select foods containing relatively high amounts of protein and low amounts of cell wall (Sedinger and Raveling 1984). Despite these preferences, proximate nutritional factors determine much of the variation in gosling growth (Würdinger 1975, Sedinger et al. 1992). Seasonal declines in availability of food and concentration of dietary protein reduces the maximum growth rate of goslings as brood-rearing progresses (Sedinger and Raveling 1986, Sedinger and Flint 1991, Cooch et al. 1991a).

However, Black Brant (*Branta bernicla*) goslings also vary substantially in growth rates among several colonies (Sedinger et al. 2001) and also among brood-rearing areas within a single colony (Herzog 2002). This variation has been attributed to variation in forage availability caused by density-dependent factors (Sedinger et al. 1998). We performed an experiment on Black Brant (hereafter, brant) goslings captured at hatch on the same day to examine the effects of variation in forage availability and habitat type on gosling growth and development. Goslings were placed on specific plots at varying intervals depending on treatment to cause variation in available biomass. We measured gosling growth and body composition to compare how variation in available biomass affected black brant goslings.

METHODS

This research was performed at the Tutakoke River brant colony on the Yukon-Kuskokwim Delta, Alaska (61°N, 165°W). Detailed descriptions of the study area can be found in Sedinger et al. (1993) and Sedinger et al. (1998). The experiment was performed in 2 separate habitat types: *Carex subspathacea* dominated grazing lawns and

slough levee. The slough levee habitat is a mixed sedge/grass community which also contains *Triglochin palustris*, a preferred food species for geese (Sedinger and Raveling 1984). A detailed description of the experiment can be found in Chapter 3.

Briefly, for this study design we collected 36, day-old goslings on June 16, 1994, from 36 randomly selected nests. We marked all goslings with unique combinations of colored plastic tarsal bands. In addition, we enclosed 18, $30m^2$ plots (9 in *C. subspathacea* grazing lawns and 9 in slough levee) in 1m tall plastic netting and randomly assigned each plot to one of three possible grazing intensities (lightly, moderately, and heavily grazed). We placed a group of 6 goslings, which were assigned to a specific treatment and habitat, on a plot every six, nine, and 12 days, respectively, to create heavily, moderately, and lightly grazed treatments.

Each group of goslings was placed in a plot every third day for 8 hours. At all other times, gosling were kept together and fed *ad libitum*. Diets were predominantly natural forage supplemented by duck chow. During inclement weather goslings were kept in a structure where they could be out of the rain.

To estimate biomass of vegetation within *C. subspathacea* grazing lawns, we removed three 10 x 10cm turves from each plot before goslings were placed on the plot, at mid-treatment (after 4 hours), and after goslings were removed. All aboveground biomass was clipped to ground surface within 24 hours of harvest, washed in fresh water and dried at 60° C in a field laboratory. These samples were later re-dried and weighed at the University of Alaska, Fairbanks.

To estimate biomass of *T. palustris* within slough levee plots, five, 10 x 10cm quadrats were randomly placed within the plot. Within each quadrat, the total number of *T. palustris* plants was recorded. In addition, for each of the first 10 Triglochin plants sampled, the length of each leaf (± 1mm), and state (grazed or ungrazed) was recorded. We, later, estimated mass of each plant, using length-mass regression based on the length and mass of individual leaves from previously sampled *T. palustris* plants (Mulder unpubl. data). As for *C. subspathacea*, we estimated *T. palustris* biomass before and after each trial as well as at the midpoint.

Before each trial, we weighed goslings (±5 grams) and measured tarsi and culmens (±0.1mm). We again weighed goslings after 4 hours and again at completion of the trial after 8 hours. Before weighing, we fasted the goslings for 1 hour to reduce gut contents.

During the last 10 days of the experiment we sacrificed goslings to examine variation in body composition, as well as body size and internal morphometrics. We dissected and analyzed carcasses as described by Raveling (1979) and Sedinger (1986). This included removing all feathers (contour and down), dissecting the gosling and weighing gizzard, gizzard contents, gut contents, and right breast muscle to the nearest 0.1 g. Also, the lengths of the small and large intestine and both ceaca were stripped of contents, and then straightened and measured to nearest 0.1mm.

We fit the growth patterns of all goslings to Gompertz curves (Ricklefs 1973) of the following form:

$$W(age) = Ae^{-be^{-k(age)}}$$

where A is the asymptotic weight, b is a constant (approximately the ratio of asymptotic to initial weight, and k the growth rate constant (Ricklefs 1968, Sedinger 1986). Models were run separately for each bird, and also by treatment, by habitat, by each habitat-treatment combination, by sex, and for all data combined.

We used general linear mixed and nonlinear models for analyses (Littell et al. 1996, SAS Institute 2001) and information-theoretic methods for model selection (Burnham and Anderson 1998). Possible fixed effects for models included sex, grazing treatment pressure, and habitat. Age of gosling was included as a possible covariate. Plot was included as a random effect in the models that examined changes in mass during a trial. All models including 2-way interactions between fixed effects or 3-way interactions with a covariate were included in the set of candidate models.

RESULTS

Gosling growth and mass dynamics.- After calculating AIC_c for all sets of growth curve models, the model combining all sexes, habitats and treatments was most likely (Fig. 1). Only the model that included separate curves for each sex was considered a plausible alternative ($\Delta AIC_c = 3.46$).

We also examined mass dynamics within a trial as a function of forage availability (Fig. 2). For both habitats the change in mass was positively correlated with forage biomass at the beginning of the trial (slope=0.5742 ± 0.2630 $g/g/m^2$). The most likely model included only forage biomass as a main effect (AIC_c=2223.8). However, a model that also included habitat in the model was almost as plausible ($\Delta AIC_c = 1.2$). Goslings within *C. subspathacea* grazing lawns gained mass more rapidly than goslings

within the slough levee habitat, at comparable forage biomass levels. The results of an F-test for fixed effects in this mixed ANCOVA model, however, suggested that within this dataset habitat did not provide additional information (p=0.2244; df=2,16; F=1.63).

Development.- For all internal and most external (see below) measurements, a model with only gosling age was selected as the most likely model, given the data (Fig. 3, Fig. 4). All models that included habitat or treatment had $\Delta AIC_c >> 3$, and thus were not considered. Table 1 presents estimated least squares results for each internal measure (standardized at gosling age = 40 days) for each habitat-treatment combination. While treatment or habitat effects did not explain variation in total dry feather mass, habitat was selected in the models that examined the length of the ninth primary (Table 1).

Body composition.- We examined variation in total protein, total lipids, and total ash among all treatment-habitat combinations (Fig. 5). For all body composition variables, the most likely model included only gosling age as a main effect (Table 1).

DISCUSSION

For many of our results we did not detect variation in development of goslings, either between habitats or among grazing levels. When not on plots, goslings were fed ad-libitum. This diet consisted of pelleted alfalfa, commercial duck chow, and natural forage. While growth of goslings (both internally and externally) is dynamic and correlated with quality and quantity of the diet (Ankney 1977, Sedinger and Flint 1991, Cooch et al. 1991a, Starck and Kloss 1995, Starck 1996, Sedinger et al. 2001) goslings in the two habitats experienced different diets only 8 hours of every 3 days (11.1% of total

time). This may not be sufficient to create measurable variation in growth, especially for those measures already well developed before the initiation of the experiment.

Also, goslings, and most avian young, have evolved the ability to withstand short-term food shortages or under-nutrition and have some capacity for compensatory growth (Schew and Ricklefs 1998). The effects of more than four weeks of continuous under-nutrition can be reversed if realimentation occurs (Turner and Lilburn 1992). Nir and Nitsan (1979) performed a somewhat more comparable experiment to ours by depriving poultry chicks of any food on alternating days. While deprived chicks had slightly lower growth rates than control birds, final body size did not differ. Nir and Nitsan (1979) showed that chicks exhibited behavioral and metabolic differences when deprived to help compensate for the food shortage. Nonetheless, in the highly seasonal environment experienced by brant goslings (Sedinger and Raveling 1986, Sedinger and Flint 1991) it seems unlikely that goslings could fully compensate for numerous temporary reductions in nutrient intake in the absence of supplementary food.

There was no variation in internal morphometrics of goslings among any of the habitat and treatment combinations, but we observed a slight decline in small intestinal length with age. This has been reported in other waterfowl studies as well (Lightbody and Ankney 1984, Aubin et al. 1986) and it has been suggested that decreases in organ weights late in growth may facilitate fledging (Aubin et al. 1986). Also, goslings significantly reduced foraging time within experimental plots later during season (Herzog 2002). It is possible that gut morphology adapted to a less fibrous diet, as goslings had

access to duck chow when off plots. Thus, when intake of natural foods on plots declined the overall fiber content of the diet also declined.

There was also no variation in external measurements such as culmen and tarsus between habitats or among treatments. Because brant are precocial, and must be able to walk, feed themselves, and thermoregulate soon after hatch, development of culmen and tarsus (and leg muscles) occurs rapidly (Würdinger 1975, Ricklefs 1979, Owen 1980, Visser and Ricklefs 1995). By the time treatments began (15 days of age), average tarsus and culmen for the goslings was 56.9mm (min - 50.9; max - 61.9) and 20.0mm (min – 18.4; max – 23.1), or 79.9% and 71.1% the size at the end of the experiment, respectively. Thus, not only were goslings on plots < 15% of the time during the summer, there was also very little growth left in many external measurements once treatments began.

In contrast to other external measurements, ninth primary was significantly longer for goslings that grazed in the *C. subspathacea* grazing lawns. Protein is not stored endogenously (Blem 1990), and feather growth is linear and rapid ($\bar{x}$ = 5.1 mm/day, this study). Thus, variation in ninth primary length suggests goslings were limited in total protein when on treatment plots, and the differences in total protein that goslings assimilated during a trial, may have been sufficient to affect feather growth in the two habitats.

We could not detect any differences between habitats on ninth primary growth rate (mm/day). Eruption of the ninth primary had occurred in 70% of all captive goslings by the time treatments started (15 days old; mean age for emergence 13.8). There were

no differences among treatments or habitats in length of ninth primary for goslings at age 24. Although the average length of ninth primaries for goslings (at age 24 days) that grazed in *C. subspathacea* was larger, the difference was not significant ($P = 0.286$), and the model with only intercept had the lowest AIC_c. Thus, variation in date of eruption of the ninth primaries cannot explain between habitat differences in growth of ninth primaries. Rate of feather growth rate must have varied between habitats, and since primary feather growth began as treatments began, differences in total protein between habitats were expressed in feather growth by the end of the experiment.

From Fig.1, it is noticeable that the rate of increase in gosling growth rate has begun to decline, and goslings were near asymptotic size when collected. Sedinger and Flint (1991) estimated the asymptote of captive goslings to be 1237 g. Based on the estimated asymptotic size parameter from the Gompertz growth model, however, captive brant goslings from this experiment are larger than goslings in the wild. In fact, our estimates of asymptotic size exceed those for captive Cackling Canada Geese (*Branta canadensis minima*; males – 1341 g; females – 1223 g) (Sedinger 1986) and Lesser Snow Geese (1478 g) (Aubin et al. 1986). We believe our estimate of asymptotic size is an artifact associate with insufficient data from the asymptotic phase of growth. Placing bounds on the asymptotic growth parameter, A, to a maximum of 1400 grams, produced a slightly lower AIC_c score ($\Delta AIC_c = -0.12$) and an estimate of the relative growth rate, k, very similar to that estimated by Sedinger and Flint (Sedinger and Flint 1991) in captive brant, 0.053 vs. 0.055, respectively.

As expected, gosling mass gain was positively correlated with forage biomass (Fig. 2). We believe the difference in mass dynamics between goslings feeding within *C. subspathacea* plots and those feeding within slough levee, may indicate a difference in feeding efficiency between the two habitats. Peck rates of goslings feeding within *C. subspathacea* grazing lawns were almost twice those observed within slough levee (Herzog 2002). Goslings must include search time while feeding within slough levee habitat and thus are much less efficient foragers within slough levee at a given forage biomass.

Previous results on wild goslings show average maximal gosling growth rates for brant to be about 27 grams/day, but there is substantial variation among goslings reared in different brood-rearing areas (Herzog 2002). Growth rates of captive birds from this experiment were within the range of wild goslings (Fig. 1). We were not able to detect variation in gosling growth rates among treatments or between habitats. Because food was available at all times when goslings were off experimental plots, goslings apparently compensated for most of the detrimental effects of variation in grazing pressure. Based on our mass dynamics model (Fig. 2), forage biomass estimates of 35 - 40 g/m^2 are required to maintain maximum growth rates of goslings. Goslings with access to less forage would be expected to grow more slowly if food is limiting. Person et al. (1998) showed that there is considerable variation in forage biomass for *Carex subspathacea* grazing lawns on brood-rearing areas associated with the Tutakoke River brant colony (20 – 80 g/m^2 during mid/late summer). This variation in biomass encompasses our estimates of forage biomass needed for maximal growth. Forage biomass estimates on

brood rearing areas are positively correlated with the mass of wild goslings using those areas at approximately 30-40 days of age (Herzog 2002, Person et al. In press). Thus, results from captive goslings we report here, substantiate the hypothesis that variation in gosling size of black brant is a result of variation in available forage.

ACKNOWLEDGMENTS

We greatly appreciate C. Mulder and B. Person for providing unpublished data on *Triglochin palustris* lengths and weights. We acknowledge the field assistance of M. Eichholz, T. Obritschkewitsch, B. O'Connell, B. Person for both care of goslings and vegetative sampling. Financial support was provided by National Science Foundation grant (OPP 92 14970). Additional logistical support was provided by the U.S. Geological Survey, Yukon-Kuskokwim Delta National Wildlife Refuge, and the Department of Biology and Institute of Arctic Biology at the University of Alaska Fairbanks.

LITERATURE CITED

Ankney, C.D. 1977. Feeding and digestive organ size in breeding Lesser Snow Geese. Auk 94:275-282.

Aubin, A.E., E.H. Dunn, and C.D. MacInnes. 1986. Growth of Lesser Snow Geese on arctic breeding grounds. Condor 88:365-270.

Blem, C.R. 1990. Avian energy storage. Pages 59-114 *in* Current Ornithology (Power, D.M., ed.). Plenum Press, New York.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference : A practical information-theoretic approach. Springer, New York.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Herzog, M.P. 2002. Environmental regulation of growth in black brant. Ph.D. Dissertation. University of Alaska Fairbanks.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619-636.

Lepage, D., G. Gauthier, and A. Reed. 1998. Seasonal variation in growth of greater snow goose goslings: The role of food supply. Oecologia 114:226-235.

Lightbody, J.P., and C.D. Ankney. 1984. Seasonal influence on the strategies of growth and development of Canvasback and Lesser Scaup ducklings. Auk 101:121-133.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.

Manseau, M., and G. Gauthier. 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74:2045-2055.

Nir, I., and Z. Nitsan. 1979. Metabolic and anatomical adaptations of light-bodies chicks to intermittent feeding. British Poultry Science 20:61-71.

Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd, London.

Owen, M., and J.M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Person, B.T., C.A. Babcock, and R.W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific black brant geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243-259.

Person, B.T., M.P. Herzog, R.W. Ruess, J.S. Sedinger, R.M. Anthony, and C.A. Babcock. In press. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia.

Raveling, D.G. 1979. The annual cycle of body composition of Canada geese with special reference to control of reproduction. Auk 96:234-252.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110:419-451.

Ricklefs, R.E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177-201.

Ricklefs, R.E. 1979. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. Auk 96:10-30.

SAS Institute. 2001. The SAS System for Windows. Version: 8.2.

Schew, W.A., and R.E. Ricklefs. 1998. Developmental Plasticity. Pages 288-304 *in* Avian growth and development: Evolution within the altricial-precocial spectrum (Starck, J.M. and R.E. Ricklefs, Eds.). Oxford University Press, New York.

Sedinger, J.S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management 48:1128-1136.

Sedinger, J.S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314-326.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger, J.S., M.S. Lindberg, B.T. Person, M.W. Eichholz, M.P. Herzog, and P.L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J.S., and D.G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger, J.S., and D.G. Raveling. 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55:1083-1102.

Sedinger, J.S. 1986. Growth and development of Canada Goose goslings. Condor 88:169-180.

Sedinger, J.S., M.P. Herzog, B.T. Person, M.T. Kirk, T. Obritschkewitsch, P.P. Martin, and B.A. Anderson. 2001. Large scale variation in growth of black brant goslings related to food availability. Auk 118:1088-1095.

Sedinger, J.S., C.J. Lensink, D.H. Ward, R.M. Anthony, M.L. Wege, and G.V. Byrd. 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. Wildfowl 44:49-59.

Sedinger, J.S., and D.G. Raveling. 1988. Foraging behavior of cackling Canada Goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

Sedinger, J.S., R.G. White, and W.E. Hauer. 1992. Heat increment of feeding and partitioning of dietary energy in yearling Black Brant. Canadian Journal of Zoology 70:1047-1051.

Starck, J.M., and E. Kloss. 1995. Structural responses of Japanese quail intestine to different diets. Deutsche Tierärztliche Wochenschrift 102:146-150.

Starck, J.M. 1996. Phenotypic plasticity, cellular dynamics, and epithelial turnover of the intestine of Japanese quail (*Coturnix coturnix japonica*). J. Zool., Lond. 238:53-79.

Turner, K.A., and M.S. Lilburn. 1992. The effect of early protein restriction (zero to eight weeks) on skeletal development in turkey toms from two to eighteen weeks. Poultry Science 71:1680-1686.

Visser, G.H., and R.E. Ricklefs. 1995. Relationship between body composition and homeothermy in neonates of precocial and semiprecocial birds. Auk 112:192-200.

Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends in Ecology and Evolution 7:384-388.

Würdinger, I. 1975. Vergleichend morphologische Untersuchungen zur Jugendentwicklung von *Anser*- und *Branta*-Arten. Journal fur die Ornithologie 16:65-86.

Table 4.1. Growth and development of captive Black Brant goslings. Results presented are estimated least square means and standard errors separated out for each habitat and treatment level. Age has been standardized to 40 days old.

Variable	Slough Levee			*C. subspathacea* grazing lawns		
	Grazed every 6 days	Grazed every 9 days	Grazed every 12 days	Grazed every 6 days	Grazed every 9 days	Grazed every 12 days
Tarsus (mm)	711 ± 20	743 ± 13	711 ± 14	690 ± 17	688 ± 15	733 ± 13
Culmen (mm)	283 ± 11	280 ± 7	280 ± 8	274 ± 9	279 ± 8	286 ± 7
Mass (g)	863 ± 92	957 ± 60	906 ± 65	917 ± 75	942 ± 65	980 ± 59
Feathers (dry) (g)	36.2 ± 5.7	43.6 ± 3.7	45.1 ± 4.0	42.6 ± 4.6	54.0 ± 4.0	45.9 ± 4.2
Gizzard (g)	58.9 ± 7.5	60.9 ± 4.8	61.2 ± 5.3	69.7 ± 6.1	62.9 ± 6.2	64.1 ± 4.7
Right breast (g)	17.1 ± 5.8	29.2 ± 3.7	26.0 ± 4.1	22.3 ± 4.7	28.0 ± 4.1	36.3 ± 3.6
Small Intestine (mm)	1875 ± 127	1863 ± 83	1925 ± 89	1956 ± 103	1997 ± 90	1890 ± 81
Large Intestine (mm)	83 ± 8	100 ± 5	96 ± 6	91 ± 7	98 ± 6	101 ± 5
Caeca (mm)	296 ± 22	330 ± 14	337 ± 15	319 ± 18	294 ± 15	331 ± 14
Total Protein (g)	71.83 ± 15.3	119.1 ± 11.4	119.6 ± 10.7	90.6 ± 12.4	107.7 ± 10.8	115.6 ± 9.8
Total Lipid (g)	56.8 ± 16.7	76.3 ± 12.4	64.3 ± 11.7	59.4 ± 13.5	78.7 ± 11.8	63.1 ± 10.6
Total Ash (g)	18.8 ± 2.9	25.0 ± 2.2	24.7 ± 1.9	22.6 ± 2.1	23.2 ± 1.9	28.2 ± 1.7

[a]significant difference between habitats (p= 0.0210)

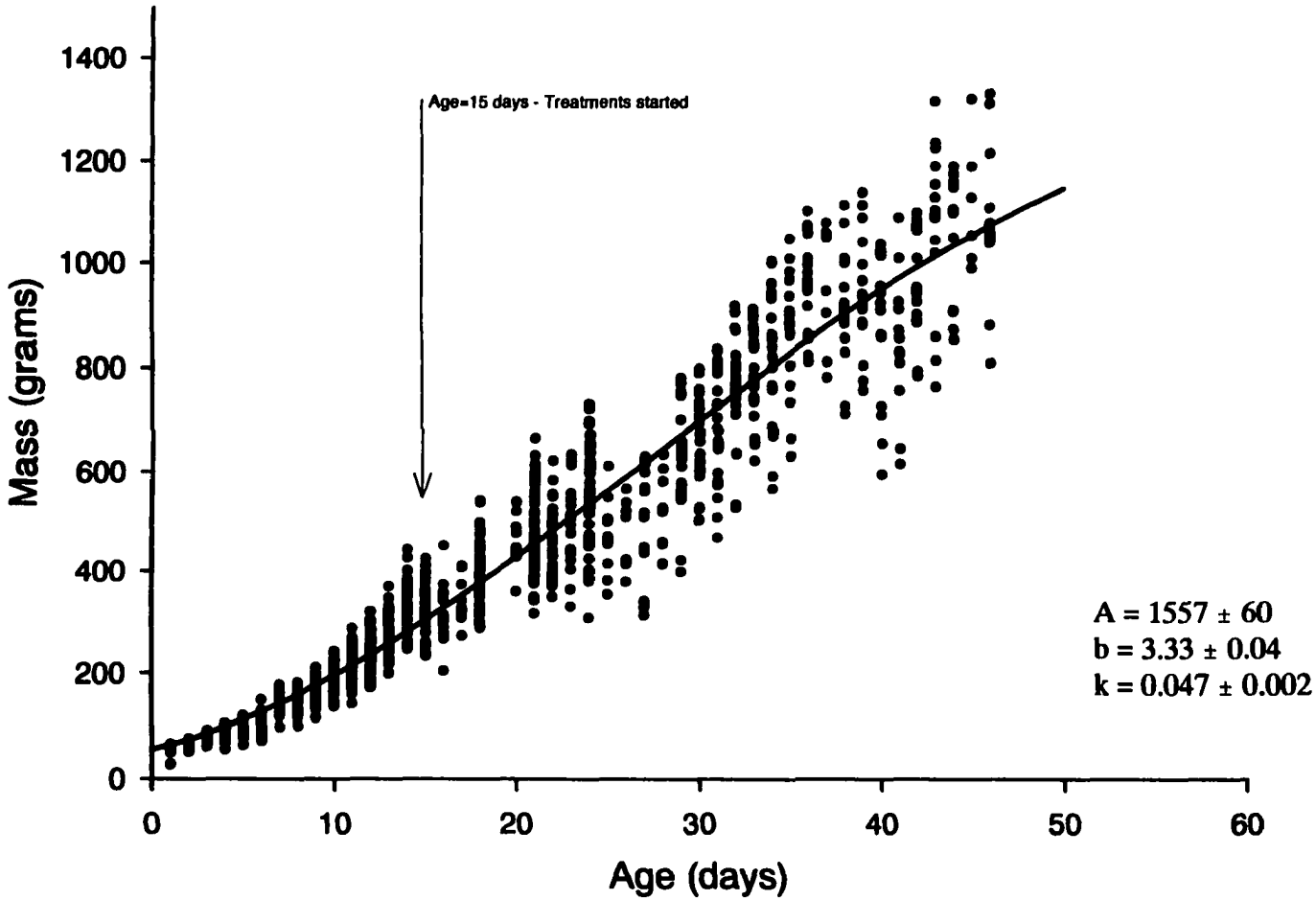

Figure 4.1. Weights of Black Brant goslings. Gosling were separated into groups of six, and treatments were started at 15 days old. Paramter estimates (±SE) and solid curve is from solution of Gompertz equation for all goslings combined.

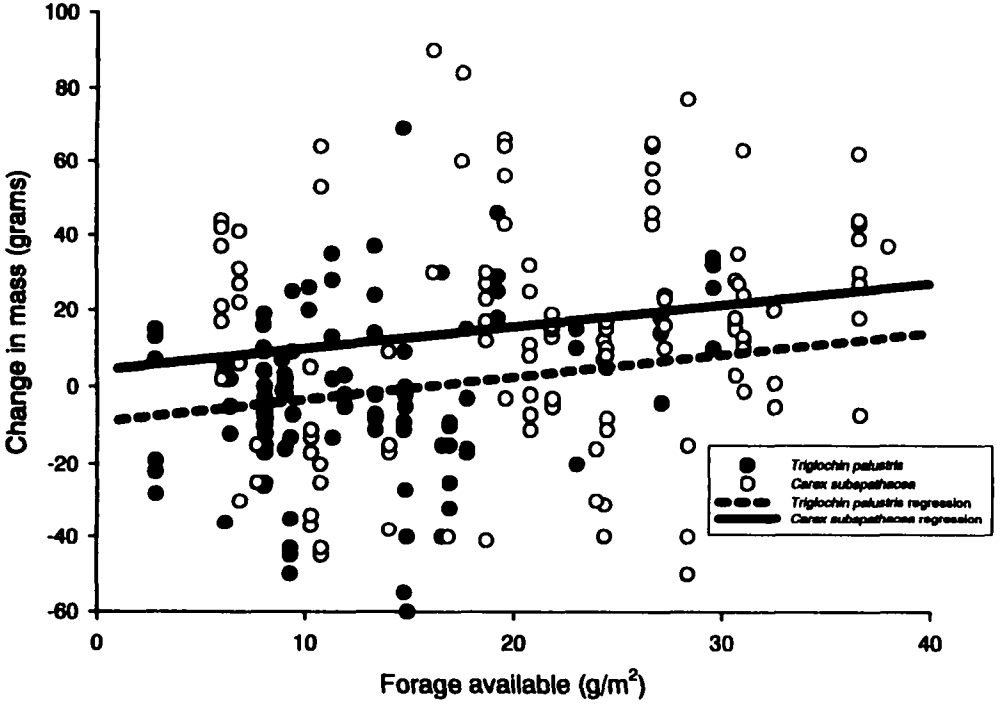

Figure 4.2. Relationship between the change in gosling mass and forage biomass during the first four hours of an eight hour trial. Open circles are measurements from goslings feeding in *Carex subspathacea* grazing lawns. Closed circles are goslings measurements from goslings feeding in slough levee habitat. Lines are the result of including habitat in model ($\Delta AIC_c = 1.2$ vs. most likely model which includes only forage biomass). Solid line represents gosling mass relationship within *C. subspathacea*, and the dashed line represents gosling mass relationship within slough levee.

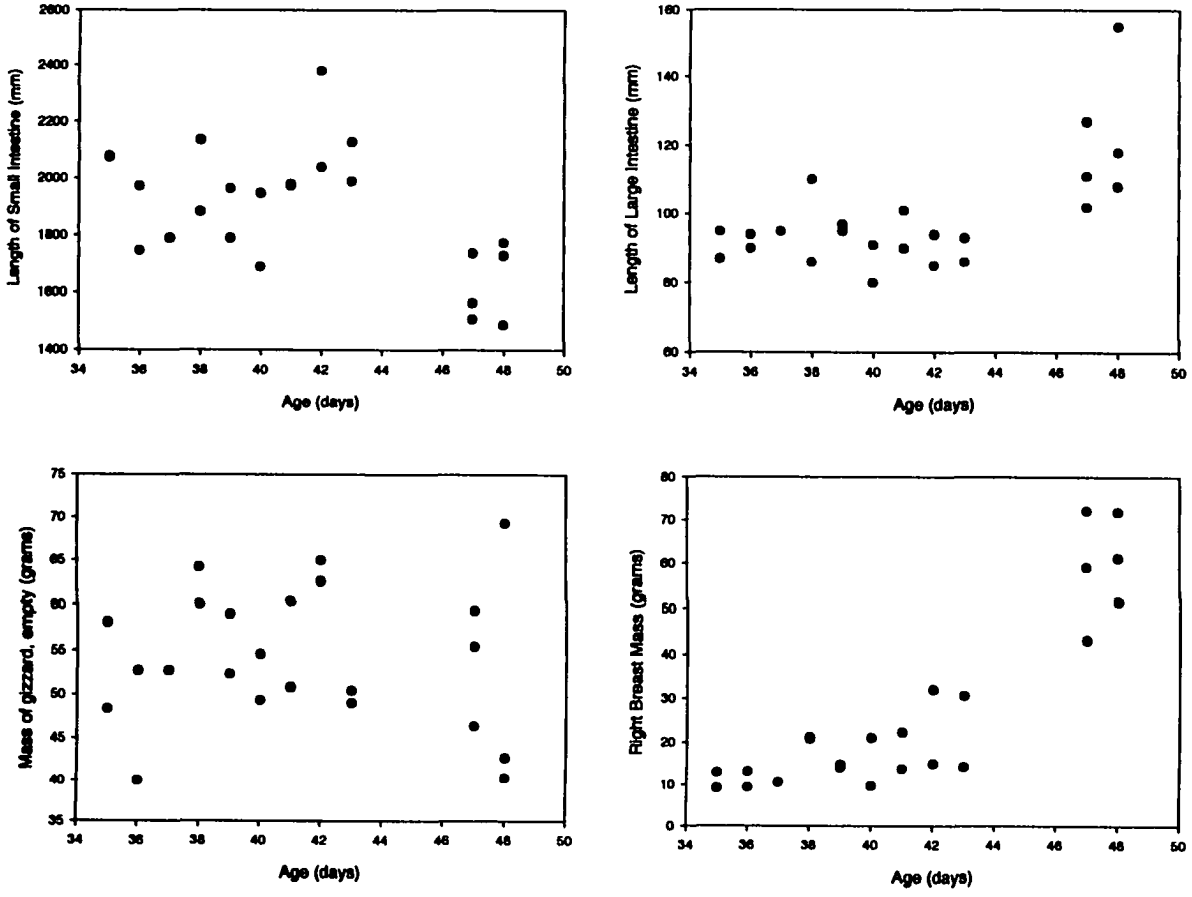

Figure 4.3. Internal morphological measurements for small intestine, large intestine, empty gizzard, and right breast muscle of captive Black Brant goslings.

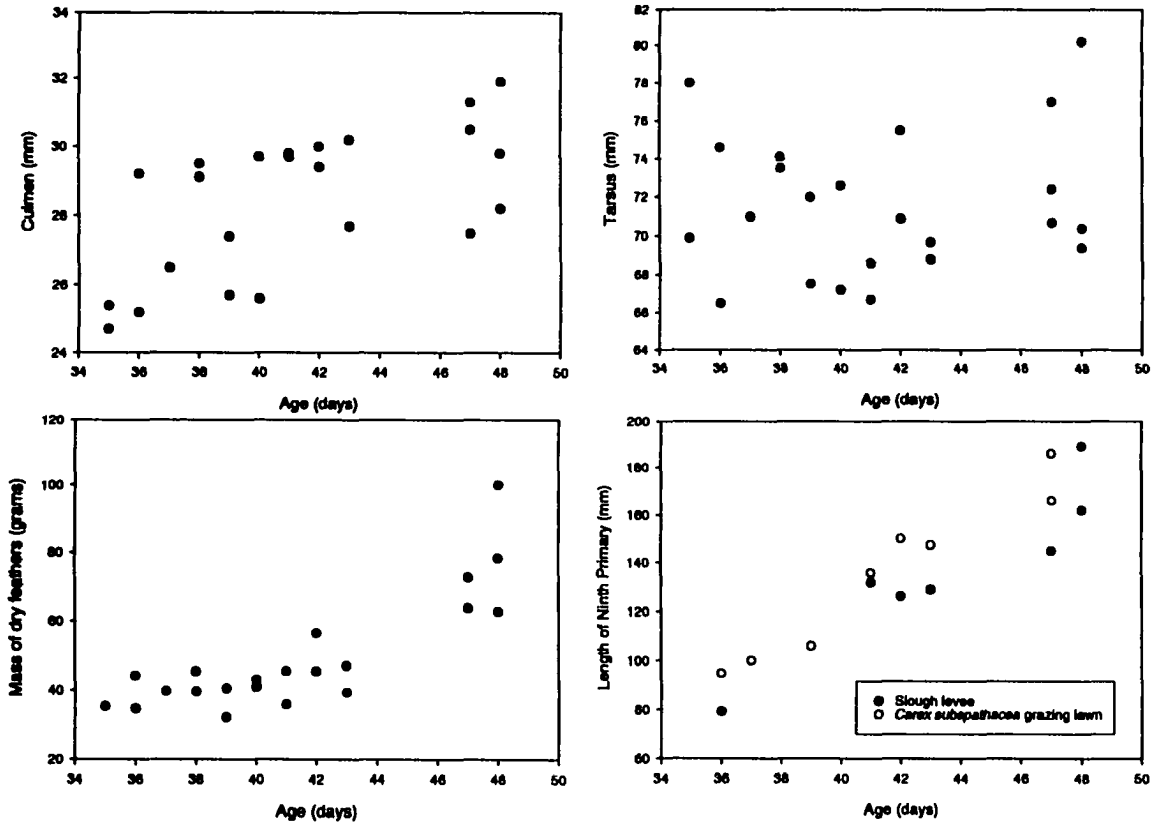

Figure 4.4. Body size and structural measurements of captive Black Brant goslings. There was a significant difference in length of ninth primary between goslings that fed in slough levee (closed circles) and goslings that fed in *Carex subspathacea* grazing lawns (open circles).

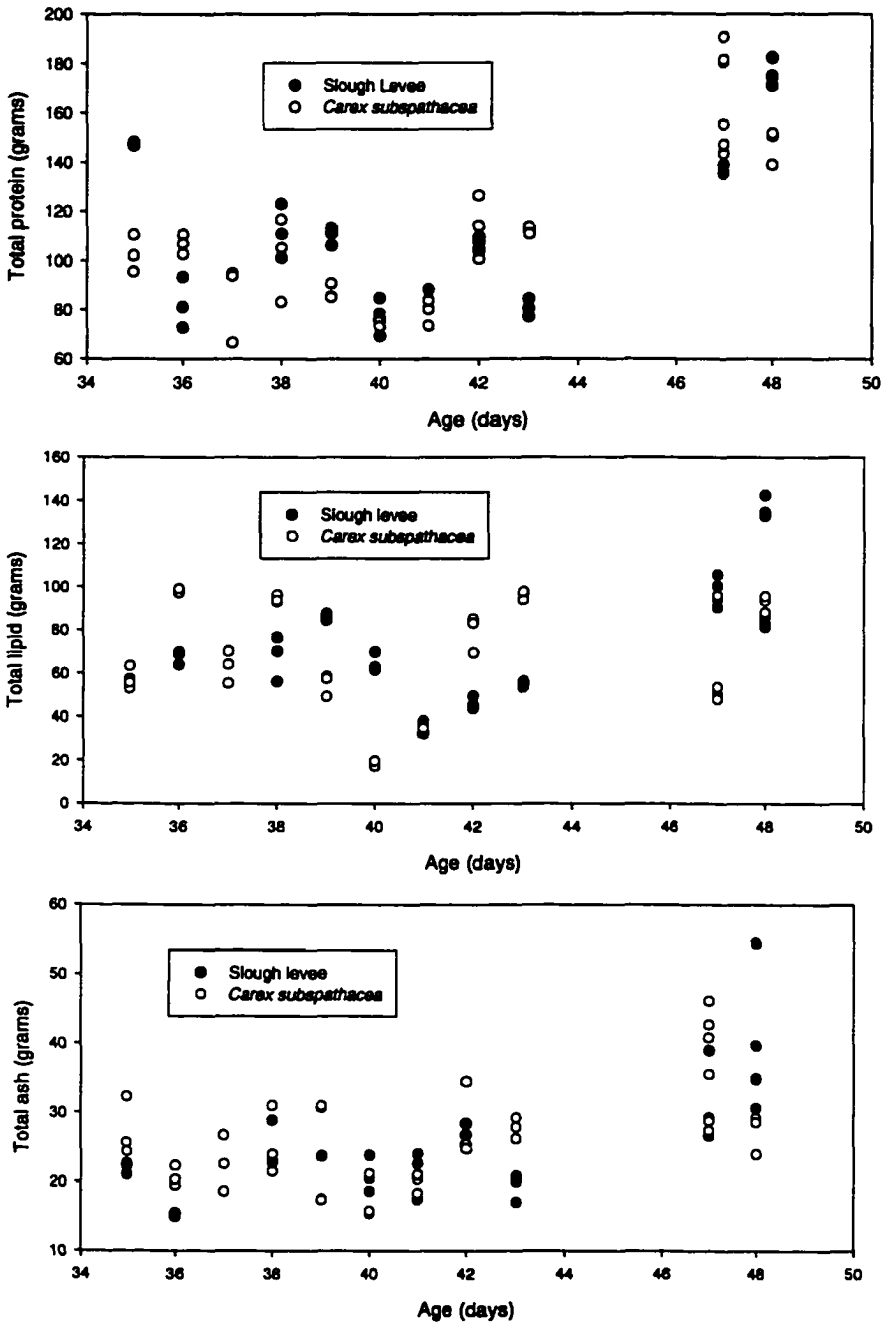

Figure 4.5. Gosling body composition results. Closed circles represent samples from goslings that fed within *Carex subspathacea* grazing lawns. Open circles represent samples from goslings within the slough levee.

Chapter 5. Spatial Variation in Gosling Growth: Interactions between Density and Forage in Black Brant (*Branta bernicla*)

ABSTRACT

Arctic nesting geese show significant variation in growth both annually and spatially. During their first summer, goslings must grow rapidly to fledge and leave the breeding grounds before food resources disappear. Variation in availability of high quality forage creates variation in growth of goslings. Because gosling size at fledging has been linked to first year survival, adult body size, and subsequent fecundity, spatial variation in quality of forage can create spatial variation in life history traits. In this paper, we examine the relationship between total forage available within a brood-rearing area, the number of birds using the area, and gosling growth. We found annual variation in use of brood-rearing areas is correlated with forage availability. It is probable that females show brood-site fidelity, but use the proximate of forage available before deciding whether to maintain fidelity, or shift areas. Also, gosling mass was negatively correlated with brood numbers when examined across all areas, however, within each brood-rearing area, the relationship between gosling mass and numbers of birds was

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Chapter 5 formatted for submittal to Auk.

positive. We did not detect a relationship between aerial estimates of availability (per m^2) and brood numbers. This suggests that spatial variation in growth among habitats may primarily be a function of habitats varying in quantity or quality of forage.

INTRODUCTION

Increased competition for a limited resource can cause declines in important life history parameters such as fecundity (Festa-Bianchet et al. 1998), survival (Clutton-Brock et al. 1987, for review see Saether et al. 1997) and final body size (Klein 1970). Arctic nesting geese hatch and rear their young in a climate with a very short growing season. Therefore, natural selection has favored rapid growth rates and rapid fledging to allow migration from breeding grounds before winter arrives (Owen 1980).

For goose species that nest in dense colonies, such as snow geese (*Chen caerulescens*), many Canada goose subspecies (*Branta canadensis*), and Black Brant (*Branta bernicla nigricans,* hereafter, "brant"), increased numbers of broods can substantially reduce per capita food availability (Cooch et al. 1991b, Sedinger et al. 1998). As the availability of forage declines, gosling growth rates decline (Sedinger and Flint 1991, Cooch et al. 1991a). At high goose densities, when available forage limits growth, spatial variation in brood numbers, or habitat quality or quantity, can translate into variation in gosling mass at the end of the season. Because body size is positively correlated with fecundity and first year survival, variation in the total amount of forage can cause significant variation in population dynamics and life history parameters (Davies et al. 1988, Alisauskas and Ankney 1990, Francis et al. 1992, Sedinger et al. 1995, Choudhury et al. 1996, van der Jeugd and Larsson 1998).

During the 1980's and early 1990's, brant on the Yukon-Kuskokwim (YK) Delta, in southwest Alaska, increased in abundance. Coincident with the increasing population, there were significant declines in gosling body size and clutch size (Sedinger et al. 1998). In addition to annual variation, there was significant spatial variation in gosling size and brood numbers. Comparable spatial variation in life history traits would be expected.

For this study, we examined data from six distinct brood-rearing areas used by brant nesting within the Tutakoke brant colony, the largest colony on the YK Delta. We examined the relationship between gosling growth and brood numbers using data collected from 1987 - 1998. We estimated biomass of two important forage species on three brood-rearing areas for three years (1996-1998) and used published estimates (1994-1995) from Person et al. (1998) to correlate spatial variation in forage abundance with our estimates of brood numbers and gosling growth rates. Variation in brood numbers and size of brood-rearing area will influence total per capita forage availability. Therefore, during 1996-1998, for three brood-rearing areas, we developed an index for total biomass of forage within each area and correlated these measures of forage availability with gosling growth and gosling numbers within the areas.

METHODS

Study area.- This research was performed at the Tutakoke River brant colony on the Yukon-Kuskokwim Delta, Alaska (61°N, 165°W). Detailed descriptions of the study area can be found in Sedinger et al. (1993), Sedinger et al. (1998), and Sedinger et al. (2001). This coastal area is characterized by low growing saltmarsh vegetation dominated by graminoids and *Carex* spp. (Kincheloe and Stehn 1991). The brood-

rearing areas are located within the nesting colony and upstream along both the Tutakoke and Kashunuk Rivers (Lindberg and Sedinger 1998). The most distant brood-rearing area we sampled in this study was the Onumtuk/Emperor Bend brood-rearing area, located 30 km up the Kashunuk River from the Tutakoke River colony.

Gosling growth.- Gosling growth estimates were provided by Herzog and Sedinger (Chapter 1). Detailed descriptions of the methods used to calculate these estimates can be found in Sedinger and Flint (1991), Sedinger et al. (2001), and Herzog and Sedinger (Chapter 1). Briefly, goslings which were initially webtagged (Alliston 1975, Sedinger and Flint 1991) from nests of marked females within one day of hatch, were captured during late summer banding drives (Sedinger et al. 1997). Gosling were weighed (± 5 g) (Dzubin and Cooch 1992), and after controlling for age of the gosling, hatch date, sex, egg size and female age, least square means estimates of gosling mass were calculated for each brood-rearing area and each year.

Estimates of brood numbers.- After hatch, brant broods leave the area of the nest and, within five days, move up to 40 km from the colony to rear their young (Flint 1993, Lindberg and Sedinger 1998). Once broods arrived at a brood-rearing area, brood movement was generally restricted to a 1-2 km home range (Flint pers. comm.). Areas from which we captured goslings were defined by natural features (major sloughs and rivers). Locations of banding drives were consistent across years, and therefore we used the same landmarks to designate brood-rearing areas. Banding drive effort (number of people per drive) was similar each year, and for this analysis we assumed that there were no differences in capture rates across brood-rearing areas. Thus, we used the number of

birds captured during the banding drive as an index of brant numbers within a specific brood-rearing area.

Forage availability.- During 1996-1998, we performed line transects within two communities *Carex subspathacea* grazing lawns and slough levee (a mixed sedge, graminoid, forb community). Transects were sampled twice each year, before hatch, and during late summer (~30-40 days after hatch). Within the *C. subspathacea* community, vegetation was continuous, and occurred along coastlines and pond margins. *C. subspathacea* grazing lawns occupy the zone between taller *C. ramenskii* and coastal mud flats. For each brood-rearing area, 10 - 20 transects were chosen randomly from color infra-red photos, and stratified to provide coverage throughout the brood-rearing area. A transect consisted of walking the perimeter of a pond or coastal margins. We recorded the coverage of *C. subspathacea* in a direction perpendicular to the shoreline approximately every 20 m. The width of the coverage was defined as the distance from the *C. ramenskii* border to the last *C. subspathacea* plant. In addition, the percent of ground covered by *C. subspathacea* was estimated visually. A transect concluded after the entire circumference of the lake was covered. For coastlines and slough shores, each transect consisted of 100 data points (approximately 2 km). Data points that did not contain *C. subspathacea* were recorded, but not included in analysis of percent cover, because these data would have inflated variances, and produced negatively biased estimates, because up to 90% of all data points within a specific transect did not contain *C. subspathacea.* We created an index for aerial extent of grazing lawns by multiplying the percent coverage by the width of the grazing lawn.

Within the slough levee community, *Triglochin palustris*, was the primary forage species (Sedinger and Raveling 1986, Mulder et al. 1996). *T. palustris* had a clumped and random distribution (Mulder et al. 1996). During 1996-1998 we performed 10 – 15, 50 m transects, in each of the three brood-rearing areas. Along each transect, at 5 m intervals, we randomly placed a 30 x 30 cm quadrat and estimated percent coverage of plant species (*Ligusticum, Chrysanthemum, Potentilla, Salvinia, Salix, Elymus, Poa, Carex*, dead cover, and bare ground). At a random corner within the quadrat, a 10 x 10cm quadrat was placed, and we removed all *T. palustris* at the ground level and recorded the length of each leaf (± 0.1 mm), number of leaves, and grazed status of each plant. We developed a length-weight regression from data provided by C. P. H. Mulder (unpublished), which was used to generate estimates of aerial biomass.

Total available biomass within a brood-rearing area.- To calculate total forage available, we used ArcView 3.2 (ESRI, Inc. 1999) and vegetation coverage maps from Tande and Jennings (1986). We calculated the total area for each brood-rearing location using the physical boundaries of the banding drives. The boundary of the coastal margin was defined by the termination of vegetation at coastal mudflats.

To estimate total *C. subspathacea* biomass, we calculated the total perimeter of all coastal, slough levee island, river, and pond margins within each area. One brood-rearing area, Kashtut, consisted of large mudflats with slough levee islands and peninsulas, surrounded by *C. subspathacea* along the perimeter. The coverages of Tande and Jennings (1986) were only detailed enough to show the largest ponds, and none of the slough levee islands. Therefore, perimeter was calculated using a planimeter. We

calculated the perimeter of all *C. subspathacea* habitat (coastal fringes, pond margins, and slough levee islands) within each brood-rearing area using detailed enlargements of color infra-red photos. Then, using a known transect distance from the Tande and Jennings (1986) coverages, planimeter measurements were converted into meters. We then multiplied the total perimeter by the estimated percent of the total perimeter that contained *C. subspathacea* calculated from our transects. To estimate an index for total *C. subspathacea* forage available for each brood-rearing area, we multiplied our biomass index, calculated previously, by the total perimeter of *C. subspathacea* within each brood-rearing area.

Because slough levee habitat was much less linear, we used the Tande and Jennings (1986) coverages and ArcView to calculate the total area of all slough levee habitat within each brood-rearing area. We compared those vegetation classifications within Tande and Jennings (1986) that corresponded most closely to our habitat descriptions based on percent coverage estimates within our transects. We eliminated any habitats within the coverages that were not consistent with habitat types that contained *T. palustris*, based on our estimates of percent cover and Tande and Jennings (1986) classifications. We multiplied the estimates of habitat area by our estimates of *T. palustris* biomass to estimate total *T. palustris* biomass for each brood-rearing area.

We examined the relationships between forage biomass and gosling mass at banding using Proc Mixed (SAS Institute 2001). Fixed effects included year, brood-rearing area, time period of sample. The number of birds and total available forage within a brood-rearing area were possible covariates. Transect, which was considered the

experimental unit, was nested within brood-rearing area and year and included as a random effect. Model selection was based on comparing probabilities of possible models using Akaike's Information Criteria (AIC_c), corrected for small sample sizes (Burnham and Anderson 1998). For models that were similarly likely ($\Delta AIC_c \leq 2$), we used model averaged estimates for parameters that were the same within models (Burnham and Anderson 1998).

RESULTS

Relationship between brood numbers and gosling growth.- There was substantial spatial and annual variation in the number of birds captured during banding drives (Fig.1) When gosling mass was regressed against number of birds captured during banding drives, there was a slight negative correlation between brood numbers and gosling growth (Fig. 2a). However, when the relationship between brood numbers and gosling growth was examined, separately, for each brood-rearing area, there was little relationship between gosling size and brood numbers in several brood-rearing areas ($0.1024 < P < 0.9264$; Fig. 2b). The trend was generally positive, however, only the Hock Slough brood-rearing area showed a significant positive relationship ($P<0.0001$)

Spatial and annual variation in forage availability.- Our estimates of the width of *C. subspathacea* grazing lawn and percent coverage varied considerably. The most likely model given our data suggested that percent coverage of *C. subspathacea* habitat varied by margin type (coast/slough margin vs. pond margin), period of brood-rearing (just after hatch vs. during fledging), and an interaction between year and period of brood-rearing (Table 1). Results from models for width of the margin, suggested a similar model as for

percent coverage, with the addition of an interaction between brood-rearing area and period (Table 1). When we examined the relationship between gosling mass and *C. subspathacea* biomass, we chose to use means and standard errors rather than least squares means, as this yielded mean biomass of *C. subspathacea* for each estimate of bird abundance. Because the type of margin (coastal or pond) was a significant factor in our models we separated perimeter estimates and percent coverages of coastal/slough margins and pond margins in both the Hock Slough and Camp brood-rearing areas (Tables 2,3).

We estimated the perimeter of available habitat and assumed that no variation existed among years (Table 4). Camp and Hock Slough contained similar perimeter estimates, whereas, the perimeter within Kashtut was significantly longer than either Camp or Hock Slough. Also, Camp and Hock Slough had very similar estimates of the percentage of margins that contained *C. subspathacea* habitat. Habitat coverage along coastal and river margins (for both Camp and Hock Slough) was substantially more continuous than along ponds. Estimates of the percentage of habitat in Kashtut along the margins of slough levee habitat were intermediate compared to ponds and coastal margins within Camp and Hock Slough brood-rearing areas.

The model most supported by our data indicated that total biomass of *C. subspathacea* varied among brood-rearing areas and time during the season (Table 1). The model which included number of birds within the brood-rearing area was nearly as likely, though the slope was not significant ($F = 0.7$, $df = 1,12$ $P = 0.4203$). The highest biomass estimates were for the Kashtut brood-rearing area (Table 5). Camp contained

slightly less forage than Kashtut, whereas Hock Slough had substantially less *C. subspathacea* than either Kashtut or Camp brood-rearing areas. Estimates of total *C. subspathacea* biomass increased during brood-rearing, and a negative relationship between the number of birds and total *C. subspathacea* biomass was present in the most likely model.

Within the slough levee habitat, the most likely model to predict aerial *T. palustris* biomass included year, brood-rearing area, and time during summer as fixed effects. Also, an interaction between time during summer and year was included in the most likely model. On a per meter basis the Hock Slough brood-rearing area contained more *T. palustris* than either the Kashtut or Camp brood-rearing areas, and Kashtut contained more *T. palustris* than Camp (Table 6). While there was an interaction between time during summer and year, *T. palustris* biomass only differed between early and late season in 1996. There was significant annual variation in both early and late summer samples.

We found that only brood-rearing area was included in the most likely model to predict total biomass of *T. palustris* (Table 1). Hock Slough had more than twice the *T. palustris* biomass, and Camp had slightly more than Kashtut (Table 8).

Relationship between numbers of birds, food available, and gosling growth.- We modeled variation in food abundance as a function of brood-rearing area, year, total forage available and numbers of birds on the brood-rearing area. Two models were almost equally likely to explain the change in *C. subspathacea* biomass between time periods (Table 1). Both models included brood-rearing area as a fixed effect. However,

number of birds on the brood-rearing area (slope = -1.25 g/bird), and also an index for total *C. subspathacea* biomass (slope = -2.89 g/g) were equally likely to be included as covariates. Within the slough levee habitat, the most likely model for predicting changes in *T. palustris* biomass, given the data, included only a positive relationship with the number of birds within the brood-rearing area (slope = 0.0061 g/bird).

We also examined the effect of year, brood-rearing area, the number of birds using the area, total *T. palustris* biomass, and an index for total *C. subspathacea* on gosling mass at the end of summer. The most likely model for these data included year, brood-rearing area, the number of birds in a brood-rearing area, and the aerial estimate of *C. subspathacea* biomass (Table 1). Gosling mass increased from 1996 to 1997, however in 1998 declined by 22% to below 1996 levels. Hock Slough had the largest goslings, slightly larger than birds caught in the Camp brood-rearing area, and 30% larger than those caught in the Kashtut area. No estimates of *T. palustris* were found to contribute significantly to models of gosling size.

DISCUSSION

During 1987-1998, the number of birds using specific brood-rearing areas varied annually, not only in absolute numbers, but also in relation to other brood-rearing areas. Variation in the total number of birds on specific brood-rearing areas in a given year is influenced by the number of that summer's nesting attempts and success (Herzog unpublished data). However, proportional differences in the number of birds within brood-rearing areas, across years, suggest that brant select which brood-rearing area to use based partially on information that varies annually. Disturbance, predators,

competition, and habitat quality are all possible determinants of habitat use by geese (Cooch et al. 1993, Hughes et al. 1994, Lindberg and Sedinger 1998). We suggest that brant exhibit fidelity to a specific brood-rearing area, at a rate relative to previous successes (Lindberg and Sedinger 1998). However, brant also respond to proximate cues of forage availability to determine the suitability of a brood-rearing area in a given year. The Kashtut brood-rearing area generally contains the largest number of broods. However, in certain years brood use declined significantly (Fig. 1). Within 1994 and 1995, comparable number of birds were captured (2228 and 2814, respectively), and Lincoln-Peterson estimates of total brood numbers for the same two years did not substantially differ (4697 ± 766, 4641 ± 596, respectively). However, we observed substantially different levels of brood use among brood-rearing areas which directly corresponded to estimates of *C. subspathacea* availability within KashTut (Fig. 1; *C. subspathacea* estimates: June 7, 1994 – 17.8 g/m^2; June 27, 1994 – 13.9 g/m^2; June 7, 1995 – 21.1 g/m^2; June 27, 1995 – 29.8 g/m^2, (Person et al. 1998)). Similarly, for 1996 - 1998, our indices for *C. subspathacea* biomass and *T. palustris* biomass were lower in 1997, than in 1996 or 1998. Also 1997, significantly fewer brant used the Kashtut brood-rearing area than 1996 or 1998.

In previous studies we have documented a negative effect of decreased forage availability on gosling mass and behavior (Herzog 2002). We have also documented that variation in growth of black brant is primarily a result of environmental variation (Herzog 2002). Our results show that during 1987-1998, there is an overall negative relationship between gosling mass and the number of birds within a brood-rearing area (Fig. 2a).

However, the negative trend does not exist when the relationship is examined for each brood-rearing area separately, and within most brood-rearing areas the trend is positive. Numerous studies have shown the positive feedbacks by grazing geese on vegetation, both through increased fertilization (Cargill and Jefferies 1984, Bazely and Jefferies 1985, Ruess et al. 1989) and stimulating primary production (Bazely and Jefferies 1985, Kotanen and Jefferies 1987, Hik 1990).

Even though increased grazing may improve forage quality for geese (lower carbon : nitrogen ratio and higher productivity), grazing still impacts total overall biomass. Within brood-rearing areas increased brood numbers reduced both *C. subspathacea* and *T. palustris* biomass. Also, Person et al. (1998) did not detect any variation in primary production across sites. Thus, variation in brant numbers can be considered a direct effect on availability of the forage among brood-rearing areas.

Variation in gosling size and food availability among brood-rearing areas in conjunction with no variation in primary production suggests variation in quantity and quality of forage across brood-rearing areas contributes to variation in growth rates of goslings. Larger goslings are found in brood-rearing areas further from the nesting area. Person et al. (1998) found an increase in the quality of forage (higher nitrogen concentrations, and lower carbon : nitrogen ratios) in brood-rearing areas further upstream within the Tutakoke study site. Thus, brood-rearing areas upstream contained fewer broods with more available forage of higher quality. Sedinger et al. (2001) found a similar relationship between growth of brant and forage biomass across colonies.

It is probable that, prior to hatch, nesting birds impact vegetation availability in brood-rearing areas located within the nesting colony. In addition, spring weather likely plays a role on forage availability at hatch. Therefore, the choice of which brood-rearing area to use may also be influenced by such factors as nesting density and weather.

At the Kashtut nesting/brood-rearing area brant respond to variation in availability of food by changing brood-rearing areas (Fig. 1). However, even in years of high brood numbers, these areas have less forage available than other areas, and also produce the smallest goslings. Potentially, trade-offs exist between choosing an area with a large number of birds and poorer habitat, and consequently creating smaller goslings, versus living in a better quality environment with less birds. Predation, is a major cause of mortality for goslings before fledging (Sargeant and Raveling 1992). Dilution, through greater numbers, is a very successful strategy to reduce the probability of being killed by a predator (Hamilton 1971, Inman and Krebs 1987). Thus, brant may be using brood-rearing areas with high numbers of broods to increase daily survival, while sacrificing over-winter survival and potentially future fecundity. Brant may increase densities on selected brood-rearing areas in years of high predation pressure, sacrificing higher growth rates and improved reproductive success for an immediate reduction in predation rates.

However, this hypothesis does not explain why brant choose to rear their young within a habitat of poor quality when habitats upstream are better. We have previously discussed possible explanations for the lack of an ideal free distribution of brant broods, with respect to growth (Lindberg and Sedinger 1998, Herzog 2002). Dispersal of goslings to brood-rearing areas occurs in the first five days after hatch. Therefore, to feed

on high quality forage, goslings need to travel up to 20 – 30 km. Without immediate or past knowledge of the habitat upstream, it seems unlikely for a parent to move goslings such a distance. Rather, fidelity to specific brood-rearing areas is more likely to be a function of a female's previous successes and failures (Lindberg and Sedinger 1998) and immediate conditions. Significant reductions in forage conditions may create the proximate incentives to switch brood-rearing areas. Females that are successful after the shift may then continue to return to the new area.

ACKNOWLEDGEMENTS

This study was funded by grants from the National Science Foundation (OPP 92 14970), Angus Gavin, and the Center for Global Change at the University of Alaska Fairbanks. Additional logistic support was provided from U.S. Fish & Wildlife Service and U. S. Geological Service. In addition, many people assisted in over 13 summers of fieldwork including N.D. Chelgren, M.W. Eichholz, P.L. Flint, D.S. Johnson, M.J. Knoche, M.S. Lindberg, W.T. O'Connell, B.T. Person, J.L. Schamber, P.A. Svete, and J.B. Wenzel.

LITERATURE CITED

Alisauskas, R.T., and C.D. Ankney. 1990. Body size and fecundity in lesser snow geese. Auk 107:440-443.

Alliston, W.G. 1975. Web-tagging ducklings in pipped eggs. Journal of Wildlife Management 45:625-628.

Bazely, D.R., and R.L. Jefferies. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22:693-703.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York.

Cargill, S.M., and R.L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology 21:669-686.

Choudhury, S., J.M. Black, and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. Ibis 138:700-709.

Clutton-Brock, T.H., M. Major, S.D. Albon, and F.E. Guinness. 1987. Early development and population dynamics in red deer. I. Density dependent effects on juvenile survival. Journal of Animal Ecology 56:53-57.

Cooch, E.G., R.L. Jefferies, R.F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: An example in the lesser snow goose. Oecologia 93:128-138.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: Evidence of environmental degradation?. Journal of Animal Ecology 60: 483-496.

Davies, J.C., R.F. Rockwell, and F. Cooke. 1988. Body-size variation and fitness components in lesser snow geese (*Chen caerulescens caerulescens*). Auk 105:639-648.

Dzubin, A., and E.G. Cooch. 1992. Measurements of geese. General field methods. California Waterfowl Thesis, Sacramento

ESRI, Inc. 1999. ArcView. Version: 3.2.

Festa-Bianchet, M., J.M. Gaillard, and J.T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367-379.

Flint, P.L. 1993. Prefledging survival and reproductive strategies in Black Brant. PhD. Thesis, University of Alaska Fairbanks. 122pp.

Francis, C.M., M.H. Richards, F. Cooke, and R.F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology 73:1346-1362.

Hamilton, W.D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31: 295-311.

Herzog, M.P. 2002. Environmental regulation of growth in black brant. Ph.D. Dissertation. University of Alaska Fairbanks.

Hik, D.S. and R.L. Jefferies. 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model.

Hughes, R.J., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536-545.

Inman, A.J., and J. Krebs. 1987. Predation and group living. Trends in Ecology and Evolution 2:31-32.

Kincheloe, K.L., and R.A. Stehn. 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim Delta, Alaska. Canadian Journal of Botany 69:1616-1627.

Kotanen, P., and R.L. Jefferies. 1987. The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. Journal of Ecology 75:961-975.

Lindberg, M.S., and J.S. Sedinger. 1998. Ecological significance of brood-site fidelity in black brant: Spatial, annual, and age-related variation. Auk 115:436-446.

Mulder, C.P.H., R.W. Ruess, and J.S. Sedinger. 1996. Effects of environmental manipulations on *Triglochin palustris*: implications for the role of goose herbivory in controlling its distribution. Journal of Ecology 84:267-278.

Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd, London.

Person, B.T., C.A. Babcock, and R.W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific black brant geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243-259.

Ruess, R.W., D.S. Hik, and R.L. Jefferies. 1989. The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23-29.

Saether, B.E., S.H. Lorentsen, T. Tveraa, R. Andersen, and H.C. Pedersen. 1997. Size-dependent variation in reproductive success of a long-lived seabird, the Antarctic petrel (*Thalassoica antarctica*). Auk 114 :333-340.

Sargeant, A.B., and D.G. Raveling. 1992. Mortality during the breeding season. Pages 396-422 *in* Ecology and management of breeding waterfowl (Batt, B.D.J., A.D.

Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, eds.). University of Minnesota Press, Minneapolis.

SAS Institute. 2001. The SAS System for Windows. Version: 8.2.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger, J.S., M.S. Lindberg, B.T. Person, M.W. Eichholz, M.P. Herzog, and P.L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J.S., and D.G. Raveling. 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55:1083-1102.

Sedinger, J.S., M.P. Herzog, B.T. Person, M.T. Kirk, T. Obritschkewitsch, P.P. Martin, and B.A. Anderson. 2001. Large scale variation in growth of black brant goslings related to food availability. Auk 118:1088-1095.

Sedinger, J.S., C.J. Lensink, D.H. Ward, R.M. Anthony, M.L. Wege, and G.V. Byrd. 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. Wildfowl 44:49-59.

Sedinger, J.S., M.S. Lindberg, E.A. Rexstad, N.D. Chelgren, and D.H. Ward. 1997. Testing for handling bias in survival estimation for black brant. Journal of Wildlife Management 61:782-791.

Tande, G. F. and Jennings, T. W. 1986.Classification and Mapping of Tundra Near Hazen Bay, Yukon Delta National Wildlife Refuge, Alaska. U.S. Fish and Wildlife Report AI 87/01.

van der Jeugd, H.P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67:953-966.

Table 5.1. Results from model selection for all analyses presented. Only models with $\Delta AIC_c \leq 2$ are included. Possible effects included margin type (slough levee, coastline, or pond shoreline), time of sampling (prior to brood use, or after ~30 days of brood use), year, brood-rearing area, estimated number of birds, aerial extent (g/m^2) and total biomass (g) of *C. subspathacea*.

RESPONSE VARIABLE	FIXED EFFECTS/COVARIATES	AIC_c	ΔAIC_c
Percent Cover of *C. subspathacea*	Margin type, time of sampling, year*time of sampling	23850.5	0.00
Width of *C. subspathacea*	Margin type, time of sampling, year*time of sampling, brood-area*time of sampling	7686.0	0.00
Index of total biomass of *C. subspathacea*	Brood-rearing area, time of sampling	202.2	0.00
	Brood-rearing area, time of sampling, number of birds	203.2	1.00
Index of total biomass of *T. palustris*	Brood-rearing area	95.5	0.00
Index of change in mass of *C. subspathacea*	Brood-rearing area, number of birds	82.9	0.00
	Brood-rearing area, total biomass of *C. subspathacea*	83.4	0.50
Gosling mass	Year, brood-rearing area, number of birds, aerial extent of *C. subspathacea*	101.3	0.00

Table 5.2. Results from *C. subspathacea* line transects (1996-1998) along shorelines (coastal and river), margins (pond and slough levee islands). Results are means (standard errors), for both sampling periods: hatch and late summer.

		Camp		Kashtut		Hock Slough	
Year	**Habitat**	**Width (m)**	**Percent Cover**	**Width (m)**	**Percent Cover**	**Width (m)**	**Percent Cover**
1996	Margins	0.58 (0.13)	42.9 (3.4)	0.47 (0.16)	47.4 (4.4)	0.30 (0.19)	39.0 (4.9)
	Shorelines	2.1 (0.42)	65.4 (11.5)	N/A	N/A	0.66 (0.45)	73.8 (12.3)
1997	Margins	0.54 (0.20)	25.7 (5.3)	0.88 (0.13)	34.8 (3.5)	0.44 (0.19)	27.8 (4.9)
	Shorelines	1.5 (0.48)	68.4 (6.4)	N/A	N/A	0.57 (0.21)	63.4 (17.4)
1998	Margins	0.89 (0.14)	37.6 (3.7)	0.53 (0.15)	27.6 (4.0)	0.28 (0.17)	38.3 (4.6)
	Shorelines	1.7 (0.62)	75.8 (12.5)	N/A	N/A	0.48 (0.22)	64.5 (24.1)

Table 5.3. Index of *C. subspathacea* biomass (per m^2), calculated as the product of percent cover of *C. subspathacea* and the width of habitat along line transects of margins (pond and slough levee) and shorelines (coast and river). Results presented are index (standard error) for three brood-rearing sampled at two times (hatch and late summer) for three years.

		Camp		Kashtut		Hock Slough	
Year	**Habitat**	**Early**	**Late**	**Early**	**Late**	**Early**	**Late**
1996	Margins	35.2 (4.83)	46.0 (4.55)	26.0 (4.12)	30.5 (3.01)	33.1 (2.44)	13.4 (2.36)
	Shorelines	131 (18.6)	169 (23.7)	N/A	N/A	N/A	47.3 (10.3)
1997	Margins	33.8 (6.51)	34.2 (5.32)	19.1 (2.65)	57.2 (5.04)	30.9 (7.98)	25.9 (7.37)
	Shorelines	124.4 (14.5)	130.7 (15.4)	N/A	N/A	43.2 (8.68)	45.1 (13.0)
1998	Margins	47.0 (5.68)	54.0 (4.98)	26.4 (5.22)	27.2 (2.43)	13.7 (2.02)	18.9 (3.30)
	Shorelines	121.3 (15.2)	194.1 (25.1)	N/A	N/A	31.8 (6.74)	33.6 (8.36)

Table 5.4. Estimates of total perimeter (km) of *C. subspathacea* habitat within three brood-rearing areas for margins (pond and slough levee island) and shoreline (coast and river). Percent habitat is the percentage of all transect data points that contained *C. subspathacea*.

	Camp			KashTut			Hock Slough		
Habitat	**Perimeter (km)**	**% Habitat**	**Final Estimate (km)**	**Perimeter (km)**	**% Habitat**	**Final Estimate (km)**	**Perimeter (km)**	**% Habitat**	**Final Estimate (km)**
Margins	83.478	33.3 (7.61)	27.798 (6.353)	84.875	61.1 (7.40)	51.859 (6.281)	60.569	34.8 (6.81)	21.078 (4.125)
Shorelines	2.540	72.3 (4.82)	1.836 (0.122)	N/A	N/A	N/A	13.003	81.6 (6.76)	10.610 (0.879)
Total	86.018		29.634 (6.475)	84.875		51.859 (6.281)	73.572		31.688 (5.004)

Table 5.5. Annual indices (1996-1998) of total *C. subspathacea* biomass available within three brood-rearing areas for margins (pond and slough levee island) and shoreline (coast and river).

		Camp		KashTut		Hock Slough	
Year	**Habitat**	**Early**	**Late**	**Early**	**Late**	**Early**	**Late**
1996	Margins	978.5	1279	1348	1582	697.7	282.4
	Shorelines	240.5	310.3	N/A	N/A	N/A	501.9
	Total	**1219**	**1589**	**1348**	**1582**	**N/A**	**784.3**
1997	Margins	939.6	950.7	990.5	2966	651.3	545.9
	Shorelines	228.4	240.0	N/A	N/A	458.4	478.5
	Total	**1168**	**1190**	**990.5**	**2966**	**1110**	**1024**
1998	Margins	1307	1501	1369	1411	288.8	398.4
	Shorelines	222.7	356.4	N/A	N/A	337.4	356.5
	Total	**1529**	**1857**	**1369**	**1411**	**626.2**	**754.9**

Table 5.6. *T. palustris* biomass (per m^2), based on line transects within three brood-rearing areas. Biomass was estimated using a length-weight regression (Mulder, C.P.H. unpublished data). Results presented are index (standard error) for three brood-rearing sampled at two times (hatch and late summer) for three years (1996-1998).

	Camp		Kashtut		Hock Slough	
Year	Early	Late	Early	Late	Early	Late
1996	0.65 (0.12)	1.7 (0.22)	1.5 (0.18)	3.2 (0.35)	1.7 (0.72)	3.9 (0.49)
1997	1.4 (.18)	1.4 (0.16)	1.0 (0.14)	1.6 (0.26)	2.1 (0.28)	1.6 (0.26)
1998	2.1 (0.43)	1.9 (0.37)	1.2 (0.16)	1.3 (0.23)	2.0 (0.38)	2.5 (0.49)

Table 5.7. Indices of total *T. palustris* biomass available (and standard error) within three brood-rearing areas for 1996-1998.

	Camp		Kashtut		Hock Slough	
Year	Early	Late	Early	Late	Early	Late
1996	2.46 (0.24)	6.37 (0.83)	3.03 (0.36)	6.47 (0.71)	9.08 (3.85)	20.8 (2.62)
1997	3.75 (0.67)	3.75 (0.60)	2.02 (0.28)	3.24 (0.53)	11.2 (1.50)	8.55 (1.39)
1998	7.87 (1.61)	7.123 (1.39)	2.43 (0.32)	2.63 (0.47)	10.69 (2.03)	13.4 (2.62)

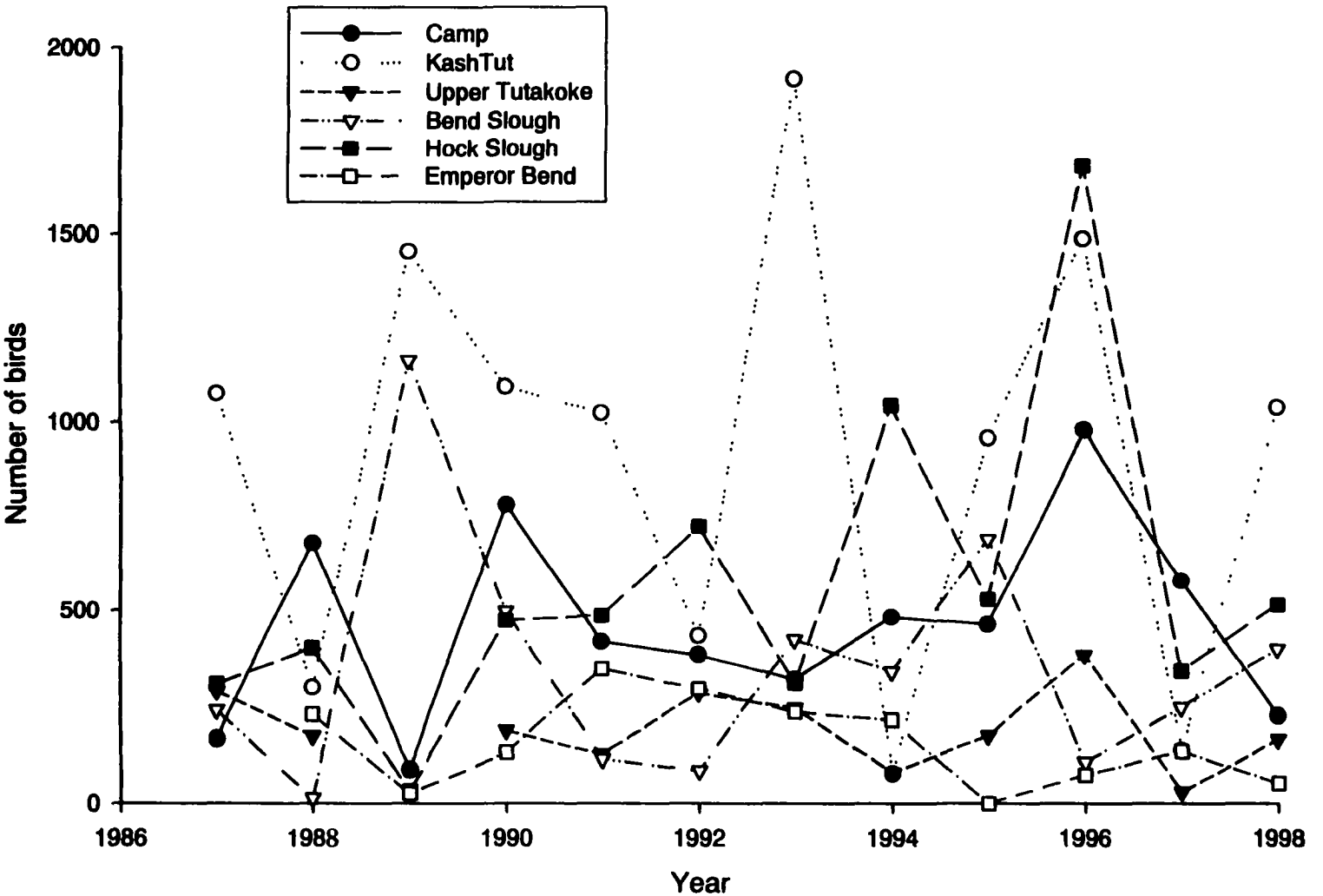

Figure 5.1. Variation in number of birds captured on six brood-rearing areas (1987-1998) during late summer banding drives.

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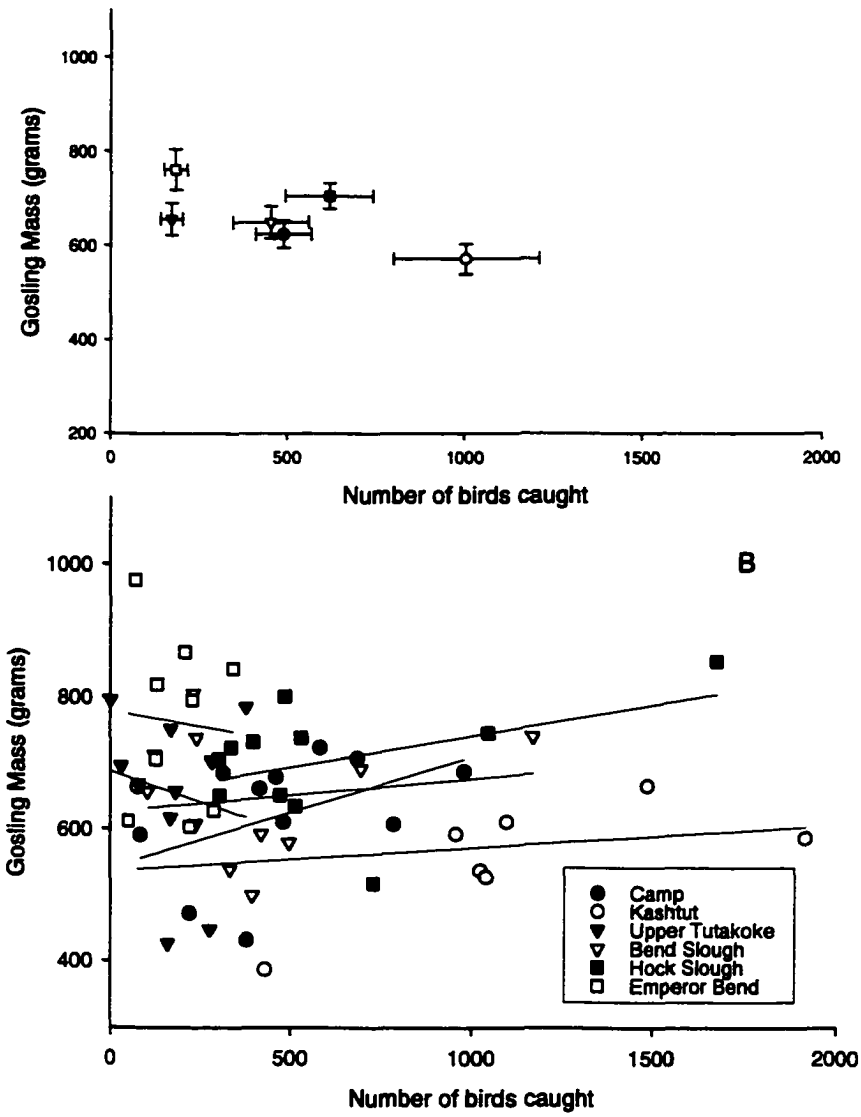

Figure 5.2. Relationship between number of birds and gosling mass (g), among all brood-rearing areas, averaged across years (A), and also analyzed separately for each brood-rearing area (B).

Chapter 6. Summary

I examined factors the influence growth in Black Brant goslings on the Yukon Kuskokwim Delta in western Alaska. Goslings grow at high rates, and consequently are very sensitive to variation in habitat quality and availability (Sedinger and Raveling 1984, Sedinger and Raveling 1986). Numerous environmental factors affect growth of goslings and final body size (Sedinger and Flint 1991, Larsson and Forslund 1991, Cooch et al. 1991a, Cooch et al. 1991b, Lindholm et al. 1994, Lesage and Gauthier 1997, Lepage and Desrochers 1999). My research not only characterized the environmental factors that influenced gosling growth, but also estimated how much of the variation was environmental versus genetic in origin. I found that nearly all variation in growth can be linked directly to environmental effects, caused primarily by spatial and annual variation in habitat quality and availability. In support of this hypothesis, my estimates of heritability were not different from zero. This is in contrast to results from Larsson and Forslund (1992) who found significant heritabilities in body size traits of Barnacle Geese. I believe that brant have been under much stronger selective pressure on body size than other geese and thus little genetic variation remains in the population.

My experiment using captive goslings is one of the few captive gosling experiments performed in the wild, and the only experiment designed specifically to examine the effects that habitat type and availability, density, and behavior of geese have on gosling growth. I found that within the *C. subspathacea* grazing lawns there was more forage available to goslings that fed within plots that experienced less grazing

pressure. Consequently, these goslings were able consume more vegetation, and gained the most weight during a trial. At the same time, goslings that were placed on heavily grazed plots, spent more time feeding, but total offtake was less than those goslings feeding on the lightly grazed plots. When feeding on *C. subspathacea* grazing lawns, gosling behavior is influenced in a complex way by date and available forage. Time spent feeding was negatively correlated with both date and forage availability. At very low levels of forage availability, there was a substantial decline in foraging behavior of goslings. This finding is in contrast to many of the observational studies on gosling behavior, that show gosling behavior varies little through time (Sedinger and Raveling 1988, Sedinger and Raveling 1990, Sedinger et al. 1995, Fowler and Ely 1997). In the wild, goslings rarely experience levels of availability less than 30 g/m^2 (Sedinger et al. 1998, Person et al. 1998) At levels of forage availability greater than 30 g/m^2, the relationship between foraging time and date is weak. Thus, date by itself, has little effect on gosling foraging behavior in the wild. Also, in contrast to the high pecking rates observed in goslings feeding on the *C. subspathacea* grazing lawns, the peck rate was very low in *T. palustris* slough levee habitat. Differences in peck rates between habitats are likely due to the differences between the feeding techniques needed within the two habitat types.

Finally, I found that annual variation in gosling growth was correlated with forage availability and gosling mass was negatively correlated with brood numbers at large spatial scales. However, within each brood-rearing area, the relationship between mass and numbers of birds was positive. I did not detect a relationship between estimates of

availability (per m^2) and brood numbers. Disturbance, predators, competition, and habitat quality are all possible determinants of habitat use by geese (Cooch et al. 1993, Hughes et al. 1994, Lindberg and Sedinger 1998). Brant exhibit fidelity to a specific brood-rearing area, in part based on previous successes (Lindberg and Sedinger 1998). However, brant also respond to proximate cues of forage availability to determine the suitability of a brood-rearing area in a given year.

I conclude that nearly all of the variation in growth that is observed within the Black Brant population at Tutakoke River (YK Delta NWR), Alaska is linked to variation in quality and availability of forage which, in turn, may be linked to the density of geese using the brood-rearing areas. For small time scales (e.g. one summer) and at large population numbers it is possible for brant to significantly reduce the availability of their forage, and consequently impact gosling growth and future fecundity.

LITERATURE CITED

Cooch, E.G., R.L. Jefferies, R.F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: An example in the lesser snow goose. Oecologia 93:128-138.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: Evidence of environmental degradation?. Journal of Animal Ecology 60: 483-496.

Fowler, A.C., and C.R. Ely. 1997. Behavior of cackling Canada geese during brood rearing. Condor 99:406-412.

Hughes, R.J., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536-545.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619-636.

Larsson, K., and P. Forslund. 1992. Genetic and social inheritance of body and egg size in the barnacle goose (*Branta leucopsis*). Evolution 46:235-244.

Lepage, D., and A.G.G. Desrochers. 1999. Seasonal decline of growth and fledging success in Snow Geese *Anser caerulescens*: an effect of date or parental quality? Journal of Avian Biology 30:72-78.

Lesage, L., and G.*. Gauthier. 1997. Growth and organ development in greater snow goose goslings. Auk 114:229-241.

Lindberg, M.S., and J.S. Sedinger. 1998. Ecological significance of brood-site fidelity in black brant: Spatial, annual, and age-related variation. Auk 115:436-446.

Lindholm, A., G. Gauthier, and A. Desrochers . 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting greater snow geese. Condor 96:898-908.

Person, B.T., C.A. Babcock, and R.W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific black brant geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243-259.

Sedinger, J.S., M.W. Eichholz, and P.L. Flint. 1995. Variation in brood behavior of black brant. Condor 97:107-115.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Sedinger, J.S., M.S. Lindberg, B.T. Person, M.W. Eichholz, M.P. Herzog, and P.L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J.S., and D.G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger, J.S., and D.G. Raveling. 1990. Parental behavior of cackling Canada geese during brood rearing: Division of labor within pairs. Condor 92:174-181.

Sedinger, J.S. 1986. Growth and development of Canada goose goslings. Condor 88:169-180.

Sedinger, J.S., and D.G. Raveling. 1988. Foraging behavior of cackling Canada Goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

Compiled Literature Cited for Entire Thesis

Alatalo, R.V., and A. Lundberg. 1986. Heritability and selection on tarsus length in the Pied Flycatcher (*Ficedula hypoleuca*). Evolution 40:574-583.

Aldrich, T.W., and D.G. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada geese. Auk 100:670-679.

Alisauskas, R.T., and C.D. Ankney. 1990. Body size and fecundity in lesser snow geese. Auk 107:440-443.

Alliston, W.G. 1975. Web-tagging ducklings in pipped eggs. Journal of Wildlife Management 45:625-628.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.

Ankney, C.D. 1977. Feeding and digestive organ size in breeding Lesser Snow Geese. Auk 94:275-282.

Ankney, C.D. 1980. Egg weight, survival, and growth of lesser snow goose goslings. Journal of Wildlife Management 44:174-182.

Aubin, A.E., E.H. Dunn, and C.D. MacInnes. 1986. Growth of Lesser Snow Geese on arctic breeding grounds. Condor 88:365-270.

Aubin, A.E., A. Dzubin, E.H. Dunn, and C.D. MacInnes. 1993. Effects of summer feeding area on gosling growth in Snow Geese. Ornis Scandinavica 24:255-260.

Barbraud, C., H. Weimerskirch, G.G. Robertson, and P. Jouventin. 1999. Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). Journal of Animal Ecology 68:1179-1192.

Bazely, D.R., and R.L. Jefferies. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22:693-703.

Black, J.M., E.G. Cooch, M.J.J.E. Loonen, R.H. Drent, and M. Owen. 1997. Body size variation in barnacle goose colonies: evidence for local saturation of habitats. Pages 129-140 *in* Research on Arctic Geese (Mehlum, F. , J.M. Black, and J. Madsen, Eds.). Norsk Polarinstitutt, Oslo.

Black, J.M., and M. Owen. 1989. Parent-offspring relationships in wintering Barnacle Geese. Animal Behavior 37:187-198.

Black, J.M., and M. Owen. 1995. Reproductive performance and assortative pairing in relation to age in Barnacle Geese. Journal of Animal Ecology 64:234-244.

Blem, C.R. 1990. Avian energy storage. Pages 59-114 *in* Current Ornithology (Power, D.M., ed.). Plenum Press, New York.

Bosque, C., and M.T. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. American Naturalist 145:234-260.

Brinkhof, M.W.G., A.J. Cave, F.J. Hage, and S. Verhulst. 1993. Timing of reproduction and fledging success in the coot *Fulica atra* - evidence for a causal relationship. Journal of Animal Ecology 62:577-587.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York.

Cargill, S.M., and R.L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology 21:669-686.

Choudhury, S., J.M. Black, and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. Ibis 138:700-709.

Clutton-Brock, T.H., S.D. Albon, and F.E. Guinness. 1988. Reproductive success in male and female red deer. Pages 325-343 *in* Reproductive Success (Clutton-Brock, T.H., Editor). University of Chicago Press, Chicago.

Clutton-Brock, T.H., M. Major, S.D. Albon, and F.E. Guinness. 1987. Early development and population dynamics in red deer. I. Density dependent effects on juvenile survival. Journal of Animal Ecology 56:53-57.

Cooch, E.G., R.L. Jefferies, R.F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: An example in the lesser snow goose. Oecologia 93:128-138.

Cooch, E.G., D. Lank, R. Robertson, and F. Cooke. 1997. Effects of parental age and environmental change on offspring sex ratio in a precocial bird. Journal of Animal Ecology 66:189-202.

Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. Ecology 72:503-512.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: Evidence of environmental degradation?. Journal of Animal Ecology 60: 483-496.

Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1992. Is there a positive relationship between body size and fecundity in lesser snow geese?. Auk 109:667-673.

Cooke, F., R.F. Rockwell, and D.B. Lank. 1995. The Snow Geese of La Pérouse Bay: Natural selection in the wild. Oxford University Press, New York.

Coulson, J.C., and C. Thomas. 1985. Differences in the breeding performance of individual kittiwake gulls, *Rissa tridactyla* (L.). Pages 489-503 *in* Behavioral Ecology: Ecological consequences of adaptive behavior (Sibly, R.M. and R.H. Smith, Eds.). Blackwell Press, London.

Davies, J.C., R.F. Rockwell, and F. Cooke. 1988. Body-size variation and fitness components in lesser snow geese (*Chen caerulescens caerulescens*). Auk 105:639-648.

Dzubin, A., and E.G. Cooch. 1992. Measurements of geese. General field methods. California Waterfowl Thesis, Sacramento

Eberhardt, L.E., R.G. Anthony, and W.H. Rickard. 1989a. Movement and habitat use by Great Basin Canada goose broods. Journal of Wildlife Management 53:740-748.

Eberhardt, L.E., R.G. Anthony, and W.H. Rickard. 1989b. Survival of juvenile Canada Geese during the rearing period. Journal of Wildlife Management 53:372-377.

ESRI, Inc. 1999. ArcView. Version: 3.2.

Falconer, D.S. 1981. Introduction to quantitative genetics, 2nd edition. Longman Inc., New York.

Festa-Bianchet, M., J.M. Gaillard, and J.T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367-379.

Findlay, C.S., and F. Cooke. 1983. Genetic and environmental components of clutch size variance in a wild population of Lesser Snow Geese (*Anser caerulescens caerulescens*). Evolution 37:724-734.

Finney, G., and F. Cooke. 1978. Reproductive habits in the snow goose: the influence of female age. Condor 80:147-158.

Flint, P.L., and J.S. Sedinger. 1992. Reproductive implications of egg-size variation in the black brant. Auk 109:896-903.

Flint, P.L., J.S. Sedinger, and K.H. Pollock . 1995. Survival of juvenile black brant during brood rearing. Journal of Wildlife Management 59:455-463.

Flint, P.L. 1993. Prefledging survival and reproductive strategies in Black Brant. PhD. Thesis, University of Alaska Fairbanks. 122pp.

Forslund, P., and K. Larsson. 1992. Age-related reproductive success in the barnacle goose. Journal of Animal Ecology 61:195-204.

Fowler, A.C., and C.R. Ely. 1997. Behavior of cackling Canada geese during brood rearing. Condor 99:406-412.

Francis, C.M., M.H. Richards, F. Cooke, and R.F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology 73:1346-1362.

Gauthier, G., R.J. Hughes, A. Reed, J. Beaulieu, and L. Rochefort. 1995. Effect of grazing by greater snow geese on the production of graminoids at an Arctic site (Bylot Island, NWT, Canada). Journal of Ecology 83:653-664.

Gustafsson, L. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. American Naturalist 128:761-764.

Hamilton, W.D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31: 295-311.

Herzog, M.P. 2002. Environmental regulation of growth in black brant. Ph.D. Dissertation. University of Alaska Fairbanks.

Hik, D.S., H.A. Sadul, and R.L. Jefferies. 1991. Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. Journal of Ecology 79:715-730.

Hik, D.S. and R.L. Jefferies. 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model.

Hipfner, J.M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. Condor 99:353-360.

Hughes, R.J., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536-545.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Inman, A.J., and J. Krebs. 1987. Predation and group living. Trends in Ecology and Evolution 2:31-32.

Jorgenson, M.T. 2000. Hierarchial organization of ecosystems at multiple spatial scales on the Yukon-Kuskokwim Delta, Alaska, USA. Arctic Antarctic and Alpine Research 32:221-239.

Kerbes, R.H., P.M. Kotanen, and R.L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: A keystone species on the west coast of Hudson Bay. Journal of Applied Ecology 27:242-258.

Kincheloe, K.L., and R.A. Stehn. 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim Delta, Alaska. Canadian Journal of Botany 69:1616-1627.

Kotanen, P., and R.L. Jefferies. 1987. The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. Journal of Ecology 75:961-975.

Lack, D. 1968. Ecological adaptation for breeding in birds. Methuen, London.

Lamprecht, J. 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). Behaviour 96:28-48.

Larsson, K. 1993. Inheritance of body size in the barnacle goose under different environmental conditions. Journal of Evolutionary Biology 6:195-208.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619-636.

Larsson, K., and P. Forslund. 1992. Genetic and social inheritance of body and egg size in the barnacle goose (*Branta leucopsis*). Evolution 46:235-244.

Larsson, K., H.P. van der Jeugd, I.T. van der Veen, and P. Forslund. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. Evolution 52:1169-1184.

Leafloor, J.O., C.D. Ankney, and D.H. Rusch. 1998. Environmental effects on body size of Canada geese. Auk 115:26-33.

Leihikoinen, E. 1986. Dependence of winter survival on size in the great tit *Parus major*. Ornis Fennica 63:10-16.

Lepage, D., G. Gauthier, and A. Reed. 1998. Seasonal variation in growth of greater snow goose goslings: The role of food supply. Oecologia 114:226-235.

Lepage, D., and A.G.G. Desrochers. 1999. Seasonal decline of growth and fledging success in Snow Geese *Anser caerulescens*: an effect of date or parental quality? Journal of Avian Biology 30:72-78.

Lesage, L., and G. Gauthier. 1997. Growth and organ development in greater snow goose goslings. Auk 114:229-241.

Lightbody, J.P., and C.D. Ankney. 1984. Seasonal influence on the strategies of growth and development of Canvasback and Lesser Scaup ducklings. Auk 101:121-133.

Lindberg, M.S., and J.S. Sedinger. 1998. Ecological significance of brood-site fidelity in black brant: Spatial, annual, and age-related variation. Auk 115:436-446.

Lindberg, M.S., J.S. Sedinger, and E.A. Rexstad. 1995. Estimating nest fidelity of adult female black brant with multi-state modeling and geographic information systems. Journal of Applied Statistics 22:725-735.

Lindholm, A., G. Gauthier, and A. Desrochers . 1994. Effects of hatch date and food supply on gosling growth in Arctic-nesting greater snow geese. Condor 96:898-908.

Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology and Evolution 14:343-348.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.

Loonen, M.J.J.E., L.W. Bruinzeel, J.M. Black, and R.H. Drent. 1999. The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. Journal of Animal Ecology 68:753-768.

Loonen, M.J.J.E., K. Oosterbeek, and R.H. Drent. 1997. Variation in growth of young and adult size in Barnacle Geese *Branta leucopsis*: evidence for density dependence. Ardea 85:177-191.

Lummaa, V., and T. Clutton-Brock. 2002. Early development, survival and reproduction in humans. Trends in Ecology and Evolution 17:141-147.

Lynch, M. and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Inc., Sunderland, MA.

Manseau, M., and G. Gauthier. 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74:2045-2055.

Mulder, C.P.H., and R.W. Ruess. 1998. Effects of herbivory on arrowgrass: Interactions between geese, neighboring plants, and abiotic factors. Ecological Monographs 68:275-293.

Mulder, C.P.H., and R.W. Ruess. 2001. Long-term effects of changes in goose grazing intensity on arrowgrass populations: a spatially explicit model. Journal of Ecology 89:406-417.

Mulder, C.P.H., R.W. Ruess, and J.S. Sedinger. 1996. effects of environmental manipulations on *Triglochin palustris*: implications for the role of goose herbivory in controlling its distribution. Journal of Ecology 84:267-278.

Neter, J., W. Wasserman, and M.H. Kutner. 1990. Applied linear statistical models, 3rd Edition. Richard D. Irwin, Inc.,

Nilsson, J.-A. 1990. Establishment success of experimentally delayed juvenile Marsh tits *Parus palustris*. Ethology 83:73-79.

Nir, I., and Z. Nitsan. 1979. Metabolic and anatomical adaptations of light-bodies chicks to intermittent feeding. British Poultry Science 20:61-71.

Nisbet, I.C.T., J.A. Spendelow, J.S. Hatfield, J.M. Zingo, and G.A. Gough. 1998. Variations in growth of Roseate Tern chicks: II. Early growth as an index of parental quality. Condor 100:305-315.

Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd, London.

Owen, M., and J.M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Owen, M., J.M. Black, and H. Liber. 1988. Pair bond formation and timing of its formation in Barnacle Geese. Pages 23-37 *in* Waterfowl in Winter (Weller, M.W., Editor). Universit of Minnesota Press, Minneapolis.

Person, B.T., C.A. Babcock, and R.W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific black brant geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243-259.

Person, B.T., M.P. Herzog, R.W. Ruess, J.S. Sedinger, R.M. Anthony, and C.A. Babcock. In press. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia.

Raveling, D.G. 1979. The annual cycle of body composition of Canada geese with special reference to control of reproduction. Auk 96:234-252.

Richner, H., P. Schneiter, and H. Stirnimann. 1989. Life-History Consequences of Growth Rate Depression: An Experimental Study on Carrion Crows (*Corvus corone corone* L.). Functional Ecology 3:617-624.

Ricklefs, R.E. 1968. Patterns of growth in birds . Ibis 110:419-451.

Ricklefs, R.E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177-201.

Ricklefs, R.E. 1979. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. Auk 96:10-30.

Ricklefs, R.E., J.M. Starck, and M. Konarzewski. 1998. Internal constraints on growth in birds. Pages 266-287 *in* Avian Growth and Development: Evolution within the altricial-precocial spectrum (Starck, J.M. and R.E. Ricklefs, Eds.). Oxford University Press, New York.

Rockwell, R.F., E.G. Cooch, C.B. Thompson, and F. Cooke. 1993. Age and reproductive success in female lesser snow geese: Experience, senescence and the cost of philopatry. Journal of Animal Ecology 62:323-333.

Ruess, R.W., D.S. Hik, and R.L. Jefferies. 1989. The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23-29.

Saether, B.E., S.H. Lorentsen, T. Tveraa, R. Andersen, and H.C. Pedersen. 1997. Size-dependent variation in reproductive success of a long-lived seabird, the Antarctic petrel (*Thalassoica antarctica*). Auk 114 :333-340.

Sargeant, A.B., and D.G. Raveling. 1992. Mortality during the breeding season. Pages 396-422 *in* Ecology and management of breeding waterfowl (Batt, B.D.J., A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, eds.). University of Minnesota Press, Minneapolis.

SAS Institute. 1999. The SAS System for Windows. Version: 8.0.

SAS Institute. 2001. The SAS System for Windows. Version: 8.2.

Schew, W.A., and R.E. Ricklefs. 1998. Developmental Plasticity. Pages 288-304 *in* Avian growth and development: evolution within the altricial-precocial spectrum (Starck, J.M. and R.E. Ricklefs, Eds.). Oxford University Press, New York.

Schmutz, J.A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. Condor 95:222-225.

Schmutz, J.A., and C.R. Ely. 1999. Survival of greater white-fronted geese: Effects of year, season, sex, and body condition. Journal of Wildlife Management 63:1239-1249.

Schmutz, J.A., and K.A. Hobson. 1998. Geographic, temporal, and age-specific variation in diets of Glaucous Gulls in western Alaska. Condor 100:119-130.

Schmutz, J.A., B.J. Manly, and C.P. Dau. 2001. Effects of gull predation and weather on survival of Emperor Goose goslings. Journal of Wildlife Management 65:248-257.

Sedinger, J.S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management 48:1128-1136.

Sedinger, J.S. 1986. Growth and development of canada goose goslings. Condor 88:169-180.

Sedinger, J.S. 1992. Ecology of prefledging waterfowl. Pages 109-127 *in* Ecology and management of breeding waterfowl (Batt, D.J.B., A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, Editors). University of Minnesota Press, Minneapolis, MN.

Sedinger, J.S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314-326.

Sedinger, J.S., M.W. Eichholz, and P.L. Flint. 1995. Variation in brood behavior of black brant. Condor 97:107-115.

Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496-502.

Sedinger, J.S., P.L. Flint, and M.S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger, J.S., M.P. Herzog, B.T. Person, M.T. Kirk, T. Obritschkewitsch, P.P. Martin, and B.A. Anderson. 2001. Large scale variation in growth of black brant goslings related to food availability. Auk 118:1088-1095.

Sedinger, J.S., C.J. Lensink, D.H. Ward, R.M. Anthony, M.L. Wege, and G.V. Byrd. 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. Wildfowl 44:49-59.

Sedinger, J.S., M.S. Lindberg, M. Eichholz, and N. Chelgren. 1997. Influence of hatch date versus maternal and genetic effects on growth of black brant goslings. Auk 114:129-132.

Sedinger, J.S., M.S. Lindberg, B.T. Person, M.W. Eichholz, M.P. Herzog, and P.L. Flint. 1998. Density-dependent effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Sedinger, J.S., M.S. Lindberg, E.A. Rexstad, N.D. Chelgren, and D.H. Ward. 1997. Testing for handling bias in survival estimation for black brant. Journal of Wildlife Management 61:782-791.

Sedinger, J.S., and D.G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger, J.S., and D.G. Raveling. 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55:1083-1102.

Sedinger, J.S., and D.G. Raveling. 1988. Foraging behavior of cackling Canada Goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

Sedinger, J.S., and D.G. Raveling. 1990. Parental behavior of cackling Canada geese during brood rearing: Division of labor within pairs. Condor 92:174-181.

Sedinger, J.S., R.G. White, and W.E. Hauer. 1992. Heat increment of feeding and partitioning of dietary energy in yearling Black Brant. Canadian Journal of Zoology 70:1047-1051.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64:419-464.

Starck, J.M., and E. Kloss. 1995. Structural responses of Japanese quail intestine to different diets. Deutsche Tierärztliche Wochenschrift 102:146-150.

Starck, J.M. 1996. Phenotypic plasticity, cellular dynamics, and epithelial turnover of the intestine of Japanese quail (*Coturnix coturnix japonica*). Journal of Zoology 238:53-79.

Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.

Tande, G. F. and Jennings, T. W. 1986.Classification and Mapping of Tundra Near Hazen Bay, Yukon Delta National Wildlife Refuge, Alaska. U.S. Fish and Wildlife Report AI 87/01.

Thomas, V.G., and H.C. Peach Brown. 1988. Relationships among egg size, energy reserves, growth rate, and fasting resistance of Canada goose goslings from southern Ontario. Canadian Journal of Zoology 66:957-964.

Turner, K.A., and M.S. Lilburn. 1992. The effect of early protein restriction (zero to eight weeks) on skeletal development in turkey toms from two to eighteen weeks. Poultry Science 71:1680-1686.

van der Jeugd, H.P., and K. Larsson. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67:953-966.

Verhulst, S., and J.M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. Journal of Animal Ecology 60:269-282.

Viallefont, A., F. Cooke, and J.D. Lebreton. 1995. Age-specific costs of first-time breeding lesser snow geese. Auk 112:67-76.

Visser, G.H., and R.E. Ricklefs. 1995. Relationship between body composition and homeothermy in neonates of precocial and semiprecocial birds. Auk 112:192-200.

Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends in Ecology and Evolution 7:384-388.

Welsh, D., and J.S. Sedinger. 1990. Extra-pair copulations in black brant. Condor 92:242-244.

Würdinger, I. 1975. Vergleichend morphologische Untersuchungen zur Jugendentwicklung von *Anser*- und *Branta*-Arten. Journal fur die Ornithologie 16:65-86.

Zicus, M.C. 1981. Canada goose brood behavior and survival estimates at Crex Meadows, Wisconsin. Wilson Bulletin 93:207-217.